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# Cryptic carnivores: why feline hair makes cats (*Felis catus*) look vegan

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Stable isotope analysis is widely used to study food webs and animal trophic levels. However,  $\delta^{15}\text{N}$  values from domestic cat hair suggest an unexpectedly low trophic level or reduced isotope enrichment for these obligate carnivores. We explored two explanations: (i) an isotopic shift of cat diet toward lower  $\delta^{15}\text{N}$  values than human food, or (ii) a lower trophic discrimination factor (TDF) in cats than humans, resulting in smaller  $^{15}\text{N}$  enrichment of cat hair. Reduced TDFs may arise from protein limitation during fur growth or from a close match between dietary and body protein amino acid composition. To test these hypotheses, we analyzed the N isotope composition of cat and human food, human hair, and cat hair and whiskers. Cat hair  $\delta^{15}\text{N}$  values ( $6.63 \pm 0.13 \text{ ‰}$ ) plotted close to human vegan hair  $7.18 \pm 0.06 \text{ ‰}$ ) but were significantly lower than human omnivore hair ( $8.83 \pm 0.03 \text{ ‰}$ ). Hypothesis (i) was rejected, as cat diet  $\delta^{15}\text{N}$  values were higher than mixed human diet, whereas hypothesis (ii) was supported, with low cat TDFs averaging  $1.61 \pm 0.44 \text{ ‰}$  compared to human TDFs of  $4.73 \pm 0.09 \text{ ‰}$ . Protein limitation from seasonal coat growth was rejected, since whiskers and fur were isotopically identical. Thus, high diet quality and close amino acid matching between diet and body protein likely caused reduced trophic  $^{15}\text{N}$  enrichment. These findings indicate protein quality can outweigh protein quantity in determining trophic N isotope fractionation in domestic cats.

## KEYWORDS

<sup>15</sup>N, *Felis catus domesticus*, trophic discrimination factors, isotope discrimination, carnivore diet

## Introduction

For decades, stable isotope analysis of hair has been employed to investigate paleodietary habits, migration patterns, and nutritional signals in both human and animal populations (Macko et al., 1999; Oelze et al., 2011; Schwertl et al., 2003; O'Connell and Hedges, 1999). Analyses of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios reveal dietary information and trophic level once nutrients have been assimilated into body tissues. However, using hair in such studies necessitates

understanding both the isotopic routing of dietary nutrients (Mora, 2022) and species-specific trophic discrimination factors (TDF; given as  $\Delta^{15}\text{N}$  and  $\Delta^{13}\text{C}$ ) (Parnig et al., 2014). In vertebrates, TDFs from diet to hair usually involve substantial  $^{15}\text{N}$  enrichment, averaging  $3.1 \pm 1.3 \text{ ‰}$  (Stephens et al., 2022). Interestingly, several studies have revealed that members of the felid lineage deviate from this general pattern. For example, Montanari and Amato (2015) reported unusually low  $\delta^{15}\text{N}$  values in the hair of tigers and snow leopards, and Parnig et al. (2014) observed that isotopic signatures in felid carnivore hair do not always mirror actual trophic levels. These findings suggest that physiological or biochemical processes specific to felid nutrition may influence nitrogen isotope fractionation. The underlying mechanisms remain unclear, largely because isotope-based studies in large wild felids are limited by sample access and dietary control. Domestic cats (*Felis catus*), as obligate carnivores closely related to wild felids but maintained under well-characterized dietary conditions, provide an ideal model system to explore potential causes of this isotopic anomaly. In this study, we hence evaluated two major explanatory pathways and three underlying mechanisms that could account for unexpectedly low  $\delta^{15}\text{N}$  values in cat hair:

- i.  $^{15}\text{N}$  depletion of commercial cat diet relative to human diet, causing the domestic cat food web base to have lower  $\delta^{15}\text{N}$  values compared to human diet (hypothesis H1), and
- ii. reduced trophic N isotope fractionation between cat diet and cat hair compared to humans (hypothesis H2). For (ii), we tested two alternative scenarios underlying low diet-consumer isotope fractionation in cats:

(ii.a) the protein quantity hypothesis - protein limitation during periods of seasonal coat growth reduces amino acid catabolism and the excretion of  $^{15}\text{N}$ -depleted products such as urea; and

(ii.b) the protein quality hypothesis - a close match between the amino acid composition of the diet and the consumer's body protein allows direct routing of amino acids from diet into keratin resulting in minimal isotope fractionation.

In this study, we measured  $\delta^{15}\text{N}$  (and  $\delta^{13}\text{C}$ ) values of domestic cat hair and whiskers and cat supermarket foods along with values of human scalp hair and human supermarket food measured in a parallel study to determine how trophic level (based on plant versus animal protein consumption) affects hair isotope composition in humans and cats, and how different hair types reflect the dietary habits of cats. Following (ii.a) we expected  $\delta^{15}\text{N}$  differences between cat hair and whiskers, since whiskers grow continuously over the whole life of the cat, whereas body hair is shed periodically, and regrowth might cause dietary protein constraints. We then compared these results with hair from humans with different diet preferences (vegan, V; vegetarian, LV; omnivorous, O) and their diets, to evaluate differences in hair  $\delta^{15}\text{N}$  values between cats and humans. This comparison provides a novel perspective on the variance of trophic discrimination factors and their application in dietary and trophic-level reconstructions across species living in the same regional food web.

## Methods

The study was conducted on domestic cats (*Felis catus*) predominantly from Vienna, with additional individuals from other parts of Austria and one cat from north-west England. All cats included ( $n = 35$ ) were kept indoors and fed commercially available diets provided by their owners, with no access to wild prey. We collected samples of dorsal guard hair (body hair from the mid-back region) from all cats and vibrissae (whiskers) from a subset, as well as commercial pet food from the owners. Additional cat food was purchased from supermarkets, comprising pelleted dry and canned wet food.

In a parallel study of Austrian human diet preferences, human scalp hair was collected from volunteers (omnivores, vegetarians and vegans,  $n = 653$ ), alongside a wide variety of supermarket food items representing the most important food categories consumed by Austrian omnivores, vegetarians and vegans ( $n = 1006$ , here we include C3 plant and animal products).

Food samples were freeze-dried (Alpha 1–4 LSC Basic, Martin Christ, Osterode am Harz, Germany) and homogenized in a ball mill (Retsch MM200, Haan, Germany). Hair samples (human scalp hair and cat hair) were washed with high-purity deionized water (Milli-Q) to remove surface contaminants, air-dried at room temperature, and then cut into 2–4 mm pieces with scissors prior to isotope analysis. All samples were then weighed into tin capsules (0.2 - 0.7 mg hair, 0.4 - 1.0 mg animal-derived diet, 1.0 - 1.8 mg plant-derived diet) prior to elemental analyzer-isotope ratio mass spectrometric (EA-IRMS) analysis of C and N isotopes. The EA-IRMS system consisted of an EA-Isolink elemental analyzer coupled via a ConFlo IV interface to the Delta V Advantage IRMS (Thermo Scientific, Vienna, Austria). Instrument precision, based on repeated analyses of a mixed sucrose–glycine laboratory standard (prepared at C and N loads matching hair and food samples), was 0.08 ‰ for  $\delta^{13}\text{C}$  and 0.12 ‰ for  $\delta^{15}\text{N}$ . Analytical precision ( $1\sigma$ ) from repeated subsampling of hair keratin and food samples was  $\sim 0.15 \text{ ‰}$  ( $\delta^{13}\text{C}$ ) and  $\sim 0.20 \text{ ‰}$  ( $\delta^{15}\text{N}$ ), and long-term reproducibility from laboratory standards across runs was  $\sim 0.15 \text{ ‰}$  ( $\delta^{13}\text{C}$ ) and  $\sim 0.2 \text{ ‰}$  ( $\delta^{15}\text{N}$ ), consistent with reported EA-IRMS performance. Each sample was analyzed once (no analytical duplicates). IRMS calibration used USGS40 and USGS41 (glutamic acid) in a two-point monthly calibration, with daily one-point calibration and blank correction using the lab standard; samples and standards were matched in terms of N and C mass within each batch to maximize accuracy.

The isotopic composition of samples is given in delta ( $\delta$ ) notation (Equation 1), reflecting the isotope ratios ( $R$ ) of the sample expressed relative to an international standard (atmospheric  $\text{N}_2$  (at-air) for  $^{15}\text{N}/^{14}\text{N}$  and Vienna Pee-Dee Belemnite (V-PDB) for  $^{13}\text{C}/^{12}\text{C}$ ):

$$\delta \text{ [‰]} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000 \quad (1)$$

with  $R$  being  $R = \frac{^{15}\text{N}}{^{14}\text{N}}$  or  $\frac{^{13}\text{C}}{^{12}\text{C}}$  for samples and standards, respectively.

Trophic discrimination factors (TDF) were calculated for hair – diet differences in  $^{15}\text{N}$  ( $\Delta^{15}\text{N}$ ) as (Equation 2):

$$\text{TDF } [\Delta^{15}\text{N}, \text{‰}] = \delta^{15}\text{N}_{\text{hair}} - \delta^{15}\text{N}_{\text{diet}} \quad (2)$$

$\Delta^{15}\text{N}$  was computed as the difference between group means (mean hair – mean diet). Standard errors (SE of  $\Delta^{15}\text{N}$ ) were obtained by Gaussian error propagation of the SEs of the hair and diet means with the equation (Equation 3):

$$\sigma_{\text{TDF}} = \sqrt{\sigma_{\text{hair}}^2 + \sigma_{\text{diet}}^2} \quad (3)$$

The same propagation was used for the mixed (averaged) diet means, using respective means and standard errors ( $\sigma$  = SE) with the equation (Equation 4):

$$\sigma_{\text{mix}} = \sqrt{\sigma_{\text{comp } x}^2 + \sigma_{\text{comp } y}^2} \quad (4)$$

For cats, mean diet  $\delta^{15}\text{N}$  was the unweighted arithmetic mean of all analyzed commercial foods (dry + wet pooled;  $n = 49$ ). For humans, we first computed unweighted source means for  $\text{C}_3$  plant foods ( $2.72 \pm 0.12 \text{ ‰}$ ,  $n = 658$ ) and animal foods ( $4.88 \pm 0.12 \text{ ‰}$ ,  $n = 131$ ). We defined the human animal-derived food pool as terrestrial animal products (meat and dairy), excluding aquatic products (fish/seafood) which have higher  $\delta^{15}\text{N}$  values than terrestrial animal products. Given the uncertainty in the different food shares and the low contribution of aquatic products (particularly freshwater and marine fish) to Austrian omnivore diet (Rust et al., 2017) we refrained from calculating specific isotopic means for animal-derived human diet and multiplying them by their fractional human consumption. We similarly calculated one grand mean of plant-derived food including a wide variety of cereals, vegetables, fruits, nuts, and legumes. Then we calculated a two-source weighted human omnivore diet mean ( $\pm$  SE) using the proportion of animal protein intake (PAPI) in German omnivores (0.64, Petzke et al., 2005):  $\delta^{15}\text{N}_{\text{mixed human}} = 0.64 \cdot \delta^{15}\text{N}_{\text{animal}} + 0.36 \cdot \delta^{15}\text{N}_{\text{plant}} = 4.10 \pm 0.09 \text{ ‰}$ .

Because cats can consume fish with pet foods, we assessed how sensitive the human animal-derived food isotope signature responds to increasing seafood (salmon) contributions. We extracted human salmon isotope values from our database and summarized their  $\delta^{15}\text{N}$ , then created mixed animal-derived food bins with increasing shares of salmon (0%, 5%, 10%, 15% of items) and recomputed human animal-derived food  $\delta^{15}\text{N}$ .

Isotopic differences between human dietary habits, between cat hair and whiskers, between human and cat dietary categories, between human and cat diets, and lastly between cat and human TDFs were examined using one-way and two-way analysis of variance (ANOVA), followed by Tukey *post-hoc* tests where more than two groups existed. ANOVAs were calculated using Sigmaplot 14.5 (SYSTAT Software, Inc.) for summary statistics data based on propagated means, standard errors, and number of replicates, and using StatGraphics 19 (Statgraphics Technologies, Inc., The Plains, Virginia, USA) for raw data.

## Results

Our results revealed a clear difference in  $\delta^{15}\text{N}$  values among human dietary habits, with omnivores ( $8.83 \pm 0.03 \text{ ‰}$ , mean  $\pm$  SE,  $n = 402$ ) displaying significantly higher  $\delta^{15}\text{N}$  signatures than vegetarians ( $8.24 \pm 0.05 \text{ ‰}$ ,  $n = 138$ ) and vegans ( $7.18 \pm 0.06 \text{ ‰}$ ,  $n = 113$ ) (Figure 1; one-way ANOVA  $F_{(2, 650)} = 403.0$ ,  $P = 1.58 \times 10^{-114}$ ; Tukey HSD:  $\text{O} > \text{LV} > \text{V}$ , all  $P < 0.001$ ).

Given that cat and human diet  $\delta^{15}\text{N}$  baselines are close in absolute values (separated by  $< 1 \text{ ‰}$ ), though significantly different (cat foods  $5.00 \pm 0.41 \text{ ‰}$ ;  $n = 50$ ; mixed human diet  $4.10 \pm 0.09 \text{ ‰}$ ,  $F_{(1, 836)} = 5.99$ ,  $P = 0.015$ ; Figures 2B, C), one would expect cat hair to plot at more positive  $\delta^{15}\text{N}$ -values than human omnivores (assuming typical hair  $\Delta^{15}\text{N} \approx 3 \text{ ‰}$ ; Stephens et al., 2022). Instead, the mean cat hair  $\delta^{15}\text{N}$  was lower ( $6.63 \pm 0.13 \text{ ‰}$ ;  $n = 43$ ) than the mean human omnivore hair  $\delta^{15}\text{N}$  ( $8.83 \pm 0.03 \text{ ‰}$ ;  $n = 402$ , Figure 1; one-way ANOVA  $F_{(1, 443)} = 637.6$ ,  $P = 8.2 \times 10^{-88}$ ; mean difference =  $2.21 \text{ ‰}$ , 95% CI  $2.04\text{--}2.38$ ), indicating a reduced  $\Delta^{15}\text{N}$  in cats. Actually, cat carnivorous hair plotted below human vegan hair.

Contrary to our expectations, there was no significant difference in  $\delta^{15}\text{N}$  between the cat hair ( $6.63 \pm 0.13 \text{ ‰}$ ;  $n = 43$ ) and cat whiskers [ $6.45 \pm 0.37 \text{ ‰}$ ,  $n = 14$ , Figure 1; one-way ANOVA:  $F_{(1, 55)} = 0.34$ ,  $P = 0.564$ ; difference ( $\Delta$ ) =  $-0.18 \text{ ‰}$  (95% CI  $-0.78\text{--}0.43$ )].

Regarding dietary isotopes, there was no significant difference in poultry  $\delta^{15}\text{N}$  values between human ( $3.48 \pm 0.29 \text{ ‰}$ ,  $n = 13$ ) and cat foods (mostly wet-canned;  $3.87 \pm 0.17 \text{ ‰}$ ,  $n = 25$ ;  $F_{(1, 36)} = 1.49$ ,  $P = 0.231$ ), whereas beef showed higher values in human ( $5.67 \pm 0.22 \text{ ‰}$ ,  $n = 11$ ) than in cat foods ( $4.62 \pm 0.44 \text{ ‰}$ ,  $n = 6$ ; ANOVA  $F_{(1, 15)} = 5.68$ ,  $P = 0.031$ ;  $\Delta = 1.05 \text{ ‰}$  [ $0.11, 1.98$ ]) and salmon had lower values in cat ( $3.83 \pm 0.56 \text{ ‰}$ ,  $n = 4$ ) than human foods ( $9.48 \pm 0.78 \text{ ‰}$ ,  $n = 9$   $F_{(1, 11)} = 20.49$ ,  $P = 8.6 \times 10^{-4}$ ;  $\Delta = 5.65 \text{ ‰}$  [ $2.90, 8.39$ ]) (Figure 2A). Pure salmon samples were isotopically similar to other aquatic products (human salmon  $9.48 \pm 0.78 \text{ ‰}$ ,  $n = 9$ ; other human aquatic foods  $10.21 \pm 0.66 \text{ ‰}$ ,  $n = 30$ ; ANOVA  $F_{(1, 37)} = 0.33$ ,  $P = 0.569$ ).

Dry pelleted ( $4.53 \pm 0.21 \text{ ‰}$ ,  $n = 17$ ) and wet canned ( $5.28 \pm 0.63 \text{ ‰}$ ,  $n = 32$ ) cat food did not differ significantly in  $\delta^{15}\text{N}$  signatures (Figure 2B) (one-way ANOVA:  $F_{(1, 47)} = 0.72$ ,  $P = 0.401$ ) resulting in a gross mean of  $5.02 \pm 0.42 \text{ ‰}$ ;  $n = 49$  ( $5.00 \pm 0.41 \text{ ‰}$ ;  $n = 50$  for all cat food combined, including one item without recorded type (dry or wet cat food)).

For humans, plant- and animal-derived diet components differed significantly (Figure 2C):  $\text{C}_3$  plant-derived human food (cereals, vegetables, fruits, nuts, oil and legumes) exhibited lower  $\delta^{15}\text{N}$  ( $2.72 \pm 0.12 \text{ ‰}$ ,  $n = 658$ ) than animal-derived human food ( $4.88 \pm 0.12 \text{ ‰}$ ,  $n = 131$ ; one-way ANOVA  $F_{(1, 787)} = 63.1$ ,  $P = 6.83 \times 10^{-15}$ ; Tukey HSD: Animal –  $\text{C}_3 = 2.15 \text{ ‰}$ , 95% CI  $1.62\text{--}2.69$ ,  $P < 0.001$ ). Using the PAPI in German omnivores (0.64, Petzke et al., 2005), we estimated a mean mixed human diet  $\delta^{15}\text{N}$  of  $4.10 \pm 0.09 \text{ ‰}$  ( $n = 789$ ).

The human terrestrial animal-derived food pool averaged  $4.88 \pm 0.12 \text{ ‰}$  ( $n = 131$ ). Human-consumed salmon averaged  $9.48 \pm 0.78$

‰ (n = 9). Increasing the salmon contribution to human animal-derived food increased the  $\delta^{15}\text{N}$  values from 4.88‰ (0%) to 5.11‰ (5%), 5.34‰ (10%) and 5.57‰ (15%). Using the PAPI mentioned above (0.64) human mean mixed diet  $\delta^{15}\text{N}$  values would increase from 4.10‰ to 4.54‰, showing the maximum uncertainty from unknown aquatic product food contributions.

Thus, the mean cat diet  $\delta^{15}\text{N}$  ( $5.00 \pm 0.41$ ‰; n = 50) did not differ from the human terrestrial animal-derived pool ( $4.88 \pm 0.12$ ‰, n = 131; difference = 0.12‰, 95% CI -0.74 - 0.98; P = 0.780) but was slightly higher than the mixed human diet ( $4.10 \pm 0.09$ ‰, n = 789) by 0.92‰ ( $F_{(1,836)} = 5.99$ , P = 0.015). Therefore,  $\Delta^{15}\text{N}$  (TDF) was much lower in cats ( $1.61 \pm 0.44$ ‰) than in human omnivores ( $4.73 \pm 0.09$ ‰; difference =  $3.12 \pm 0.45$ ‰, z = 6.94, P =  $3.9 \times 10^{-12}$ ). This difference of over 3.0‰ between human and cat TDFs corresponds to one full trophic level in trophic isotope studies.

## Discussion

In this study we explored two possible explanations of why carnivorous pets such as domestic cats appear isotopically similar to humans on plant-based (vegan) diets. Contrary to our hypothesis H1,  $\delta^{15}\text{N}$  values of the main ingredients in cat and human foods purchased in Austrian supermarkets did not differ consistently (Figure 1A), contradicting our prediction that cat diets would be strongly  $^{15}\text{N}$ -depleted relative to human diets and assuming comparable TDFs across species. Our results were in line with our H2 suggesting that hair formation in cats involves minimal trophic isotope fractionation as dietary amino acids are incorporated into keratin without substantial  $^{15}\text{N}$  enrichment whereas human hair formation gives rise to greater  $^{15}\text{N}$  enrichment. Therefore, cat trophic

$^{15}\text{N}$  enrichment seems to be regulated by its animal physiology and diet quality (Vanderklift and Ponsard, 2003).

According to the protein quantity hypothesis, diets with excess nitrogen (high protein) cause large trophic isotope fractionation, whereas protein-limited diets result in low  $^{15}\text{N}$  enrichment (Sponheimer et al., 2003). Under high protein intake, a larger fraction of dietary N is excreted as  $^{15}\text{N}$ -depleted waste, leading to  $^{15}\text{N}$  enrichment of body tissues. This mechanism reflects the balance between dietary protein supply and protein demand: TDF is lower under protein limitation and higher when protein supply exceeds demand.

Domestic cats shed their coats twice a year, during winter and summer moulting, with fur replaced in a short time frame (Hendriks et al., 1997). If protein supply were limiting during these periods, seasonal fur growth could reduce  $^{15}\text{N}$  enrichment in winter or summer coats. In contrast, whiskers grow continuously throughout most of the year and are replaced when lost, typically under conditions of sufficient dietary protein intake when TDF and  $^{15}\text{N}$  enrichment in whiskers can occur. Therefore, whiskers might be expected to show higher  $\delta^{15}\text{N}$  values than seasonal fur. However, we found no difference in  $\delta^{15}\text{N}$  between cat hair and whiskers.

During the moulting, maximal hair growth is estimated at  $\sim 5$  g hair-protein  $\text{kg}^{-1}$  body mass  $\text{month}^{-1}$ , compared to the recommended daily protein intake for adult cats of  $\sim 5$  g  $\text{kg}^{-1}$  body mass  $\text{day}^{-1}$ , or 150 g  $\text{kg}^{-1}$  body mass  $\text{month}^{-1}$  (NRC-National Research Council, 2006). Thus, hair growth accounts for only 3% of daily protein intake, making protein limitation during coat replacement unlikely. Consequently, the protein quantity hypothesis can be rejected for cats. Differences in hair growth patterns – continuous vs. seasonal – did not impact protein supply-demand balance and thus did not produce differences in

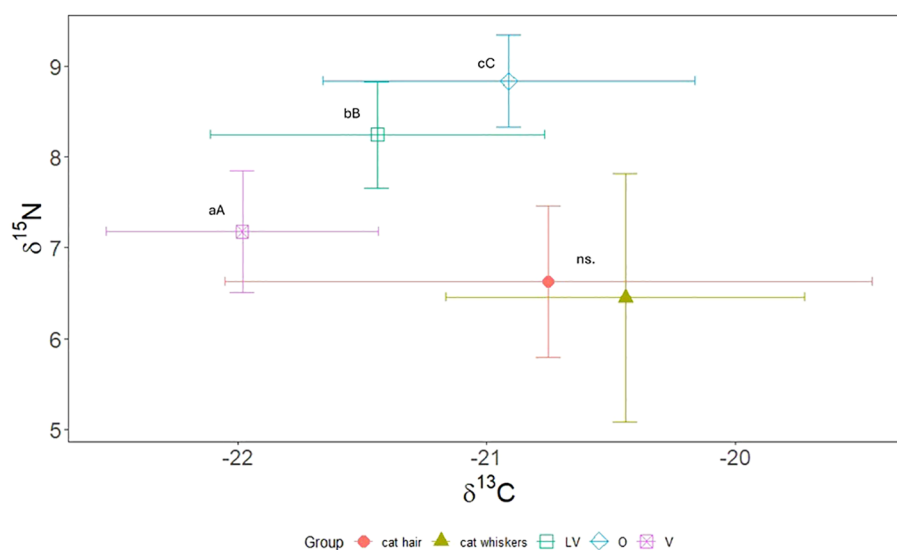
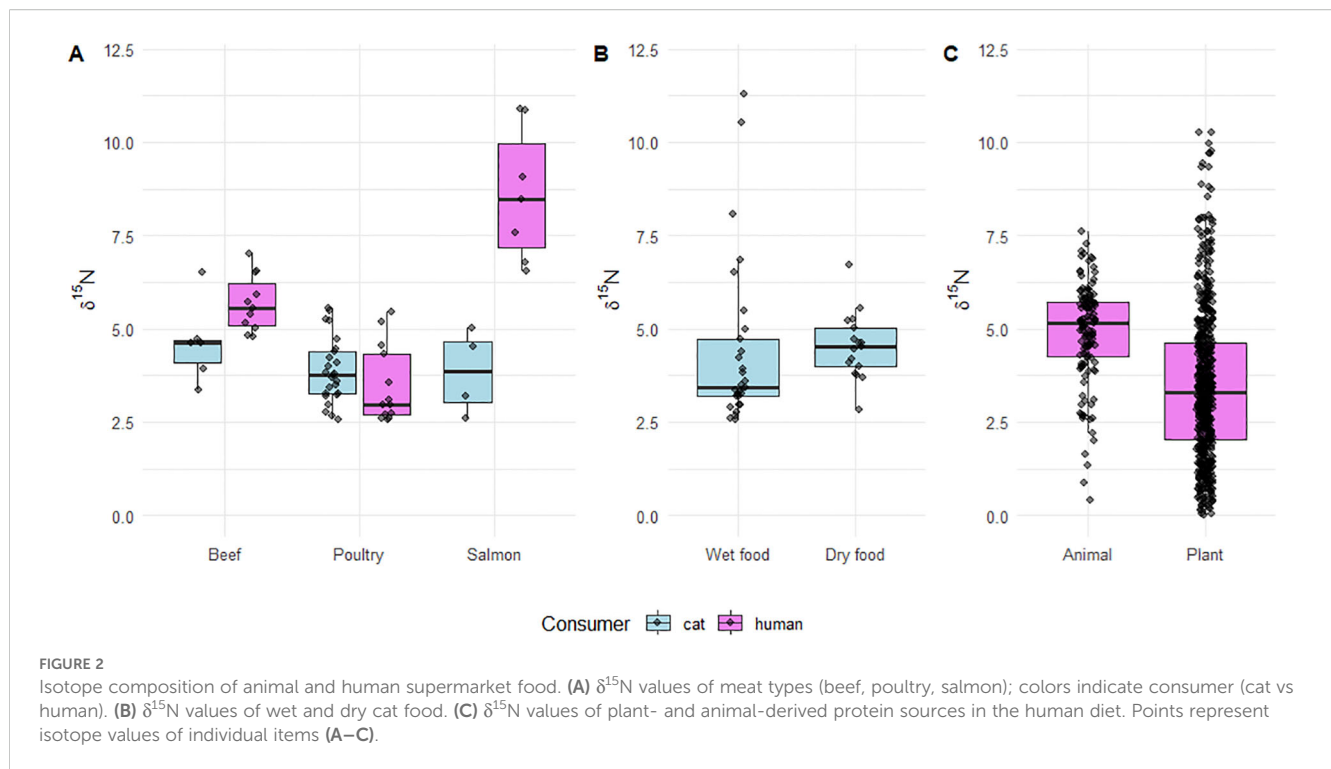


FIGURE 1

Hair isotope differences between cats and humans.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of cat hair and cat whiskers compared to scalp hair from omnivorous humans (O), vegetarians (LV) and vegans (V). Error bars show SD. Different uppercase letters indicate significant differences between human diet groups in  $\delta^{15}\text{N}$  and lowercase letters for  $\delta^{13}\text{C}$ .





TDF between hair types. The low cat TDF was therefore reflected in both whiskers and fur hair.

Instead, the low TDF in cats is more likely explained by the protein quality hypothesis. This hypothesis proposes that consumers feeding on lower quality, amino-acid-mismatching diets (e.g., herbivores consuming plant material) require greater amino acid recycling and re-synthesis, leading to higher  $^{15}\text{N}$  enrichment and higher TDF (Robbins et al., 2005). Conversely, consumers with high-quality diets closely matching their body protein composition (e.g., carnivores feeding on meat) show reduced amino acid recycling and more direct routing of amino acids from diet to body protein, which suppresses trophic  $^{15}\text{N}$  enrichment. Additionally, unlike humans, cats cannot synthesize arginine and rely on dietary intake (Morris and Rogers, 1978). Cat hair keratin contains 6.1 mol% arginine (human hair 5.8 mol%), and arginine carries four N atoms (Hendriks et al., 1998). Therefore, limited isotope fractionation during direct routing of essential amino acids including arginine in cats could lower hair  $\Delta^{15}\text{N}$  relative to humans and other vertebrates. This idea is consistent with the protein-quality framework but requires amino acid-specific  $\delta^{15}\text{N}$  measurements to evaluate.

Consistent with the protein-quality hypothesis, the most recent synthesis of mammalian hair-diet TDFs, found higher  $\Delta^{15}\text{N}$  in herbivores ( $3.7 \pm 1.3$  ‰) than in omnivores ( $2.8 \pm 1.0$  ‰) or carnivores ( $2.6 \pm 1.2$  ‰) (Stephens et al., 2022; Stephens et al., 2023). Domestic cats fed high-quality, meat-based diets provided by owners likely experience the highest possible match between dietary and body protein amino acid profiles, explaining their low  $\Delta^{15}\text{N}$  (1.61 ‰ in this study). In contrast, human vegetarians and omnivores consume mixed plant and animal protein diets, requiring more amino acid recycling and producing higher  $\Delta^{15}\text{N}$  (4.73 ‰ in this study).

Similar trends have been observed in ruminants, where diets with higher efficiency of nitrogen utilization (ENU; animal N gain per dietary N intake) produce lower  $\Delta^{15}\text{N}$  values (Cantalapiedra-Hijar et al., 2015). This effect is linked to greater partitioning of dietary nitrogen into anabolic rather than catabolic pathways and lower hepatic urea synthesis (urea being  $^{15}\text{N}$ -depleted).

Differences in dietary protein quality across studies likely also explains the wide range of  $\Delta^{15}\text{N}$  values reported for felids: domestic cats had  $\Delta^{15}\text{N}$  values between  $1.9 \pm 0.7$  ‰ ( $n = 9$ ; Cecchetti et al., 2021),  $1.9$  ‰ ( $n = 1$ ; McDonald et al., 2020), and  $2.8 \pm 0.4$  ‰ ( $n = 14$ ; Maeda et al., 2019), while wild felid cats exhibited  $\Delta^{15}\text{N}$  values from  $-0.3$  to  $0.3$  ‰ in tigers and snow leopards ( $n = 17$ ; Montanari and Amato, 2015),  $2.5$  ‰ in lions and leopards ( $n = 5$ ; Mutirwara et al., 2018), and from  $3.5$  to  $4.6$  ‰ in African lions, bobcats, and mountain lions ( $n = 8$ ; Parnig et al., 2014).

Carbon isotope values in domestic and wild cat food differ due to the absence of  $\text{C}_4$  plant inputs in wild cat diets at northern latitudes, whereas domestic cat food shows higher  $\delta^{13}\text{C}$  values. This enrichment is likely driven by the inclusion of  $\text{C}_4$ -derived feed (e.g., maize silage or seed) in livestock and poultry farming, which is subsequently reflected in the hair of domestic cat consumers (Cove et al., 2018; McDonald et al., 2020). However, in this study we focused on differences in nitrogen isotopes, which typically provide a more reliable indicator of trophic level when trophic discrimination factors (TDFs) are known or are consistent across species.

## Conclusion

In conclusion, the reason carnivorous cats isotopically resemble vegan humans is their very low  $\Delta^{15}\text{N}$ , likely driven by an almost

perfect match between dietary and body protein amino acid composition, minimizing trophic  $^{15}\text{N}$  enrichment. Differences in diet quality between feral, stray, and domestic cats—ranging from wild prey to mixed farm prey to high-quality provisioned diets—can produce substantial variation in TDF, which must be considered in studies of cat impacts on wildlife (e.g., Maeda et al., 2019; McDonald et al., 2020; Cecchetti et al., 2021; Cove et al., 2018).

Similarly,  $\Delta^{15}\text{N}$  values derived from captive or pet animals fed high-quality commercial diets may not accurately represent values for free-ranging felids on natural diets, potentially biasing isotope-based dietary models. Future work should focus on identifying proxies for diet digestibility, protein quality, and amino acid profile matching between diet and consumer proteins, and relating these to variation in  $\Delta^{15}\text{N}$  (and  $\Delta^{13}\text{C}$ ) to improve predictions of protein quality and quantity effects on trophic discrimination factors.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, and cat hair and cat diet raw data are available in [Supplementary Table 1](#).

## Ethics statement

Ethical approval was not required for the studies involving humans because the study involved the voluntary, anonymous donation of small samples of human scalp hair obtained during routine grooming. No invasive procedures were performed, no identifying information was collected, and no harm or distress was caused to human participants. In line with the University of Vienna's guidelines and Austrian national regulations, this type of non-invasive and anonymous human hair sampling does not require prior review or formal approval by an ethics committee. Accordingly, this study is considered exempt from formal ethics approval. Ethical approval was also not required for the studies involving domestic cats in accordance with the local legislation and institutional requirements. Hair sampling was non-invasive, painless, and posed minimal to no risk to the animals: hair was collected during routine grooming/handling and with the consent of the owner, without sedation or restraint beyond that normally encountered in care, and therefore no harm or distress was caused to animals. In line with the University of Vienna's guidelines and Austrian national regulations, this type of non-invasive animal hair sampling does not require prior review or formal approval by an ethics committee. Accordingly, this study is considered exempt from formal ethics approval.

## Author contributions

VZ: Writing – original draft, Writing – review & editing. MT: Writing – original draft, Writing – review & editing. HR: Writing – original draft, Writing – review & editing. WW: Writing – original draft, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1699291/full#supplementary-material>

### SUPPLEMENTARY FIGURE 1

Human scalp hair isotope values by diet. (A)  $\delta^{13}\text{C}$  (‰), and (B)  $\delta^{15}\text{N}$  (‰) for omnivores (O), lacto-ovo vegetarians (LV), and vegans (V). Points are individual samples;  $\delta^{15}\text{N}$  clearly separates human dietary habits (O highest, LV intermediate, V lowest), consistent with decreasing animal-derived protein contributions across groups;  $\delta^{13}\text{C}$  shows a parallel stepwise  $^{13}\text{C}$  depletion

from  $O \rightarrow LV \rightarrow V$ . Sample sizes:  $O$ ,  $n = 402$ ;  $LV$ ,  $n = 138$ ;  $V$ ,  $n = 113$ . For  $\delta^{15}N$ , one-way ANOVA  $F_{(2,650)} = 403.0$ ,  $P = 1.58 \times 10^{-114}$ ; Tukey HSD:  $O > LV > V$  (all  $P < 0.001$ ).

#### SUPPLEMENTARY TABLE 1

Raw data points (code, species, sample type, year,  $\delta^{15}N$ ,  $\delta^{13}C$ ) for cat hair and whiskers.

#### SUPPLEMENTARY TABLE 2

Summary statistics (mean, standard deviation, sample size ( $n$ )) of  $\delta^{15}N$  and  $\delta^{13}C$  signatures for human food items for the levels (a) category ("animal & products, plant, seafood") and (b) class ("Cereal\_C3, Cereal\_C4, Fruits, Legumes, Vegetable, Fungi, Meat, Dairy, Fish") and (c) human hair following different dietary habits ("vegetarian (LV), omnivore (O), vegan (V)")

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