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RESEARCH ARTICLE

Seasonal Profile of Glucose, Triglycerides and Urea in Two *Peromyscus* Species (Rodentia: Cricetidae) in a Mid-Latitude Temperate Coniferous Forest

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Abstract

Plasma levels of glucose, triglycerides, and urea were evaluated as indicators of intermediary metabolism (IIM) in adult males of two free-living wild mouse species of the genus *Peromyscus*, inhabiting a mid-latitude temperate coniferous forest. While seasonal IIM profiles were generally similar regardless of body size, notable differences emerged during the periods of peak reproductive activity for each species. Environmental factors such as daylight hours and temperature could influence IIM seasonally. Spatiotemporal assessment of IIM offers a simple, reliable, and low-cost method for understanding of the individuals' metabolic patterns of the species under study. This approach provides an additional tool for exploring the energy requirements of free-living wild species from an ecophysiological perspective and can complement diet studies.

Keywords: *Peromyscus*, Mice, Glucose, Triglycerides, Urea, Metabolism, Environmental Factors, Reproduction.

1. Introduction

Small terrestrial mammals obtain carbohydrates, lipids, and proteins from their diet (e.g., fungi, plants, arthropods, among other sources). These biomolecular groups are essential for acquiring metabolic energy, which enables various physiological processes throughout their ontogeny (Grodzinski & Wunder, 1975). Some carbohydrates serve as short-term energy sources (e.g., glucose), while others function as structural components (e.g., chitin) (Nelson & Cox, 2005). Lipids act as structural molecules (e.g., membranes), precursors for hormone synthesis (e.g., sex steroids and corticosteroids), and medium- to long-term energy reserves (Nelson & Cox, 2005). Proteins may function as enzymes that catalyze biochemical reactions, provide structural or mechanical support, and participate in cell communication, immune responses, cell adhesion, and the cell cycle, among other roles (Nelson & Cox, 2005).

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The relationships between the three groups of biomolecules are integrated into the so-called intermediary metabolism (IM). IM can be defined as the set of chemical reactions involved in the biotransformation of carbohydrate, lipid, and protein molecules present as nutrients in food to obtain metabolic energy. IM is linked to the life strategies of organisms, which, through their diet, cover their energy requirements by consuming nutrients. This is associated with the catabolism (i.e., degradation) and anabolism (i.e., synthesis) of monosaccharides, amino acids, fatty acids, and related compounds (Cardellá-Rosales et al., 2020). Overall, IM is another dimension of a species' niche, which, when quantified, can be an effective method for biochemically explaining the processes that define the interactions of animal species with their environment.

Reproduction in animals is closely linked to food availability, which in turn depends on environmental factors such as photoperiod, temperature, and rainfall (Sadleir, 1969; van Tienhoven, 1983; Bronson, 1989). IM, which supports the energy demands of reproduction and its associated costs, is influenced by seasonal changes that affect resource abundance. This relationship is particularly evident in regions with pronounced seasonal variation or wet-dry cycles. In small terrestrial mammals inhabiting temperate zones of the Northern Hemisphere, reproductive activity typically peaks in summer and declines or ceases in winter (Sealander, 1951; Dunmire, 1960; Hayward, 1965; Smith & McGinnis, 1968; Dark et al., 1983; Hill, 1983; Bronson, 1989; Merritt et al., 2001).

As a model for studying the biology of free-living wild rodents in mid-latitude temperate coniferous forests, we focused on populations of *Peromyscus melanotis* and *P. difficilis*. For both species, spatial and temporal dynamics have been documented at the study sites, including the influence of biotic and abiotic factors on microhabitat heterogeneity, overall and sex-specific frequency, and aspects of reproductive biology from an endocrine perspective (e.g., Castro-Campillo et al., 2008, 2012; De-La-Cruz et al., 2019, 2021; Salame-Méndez et al., 2019, 2024). These studies prompted questions about whether environmental factors influence their energetic biochemistry and whether such influences help explain interspecific reproductive differences—potentially related to body size.

Peromyscus melanotis is significantly smaller in size and weight than *P. difficilis* (2/1.5 times, respectively), and considering that the physiological activities associated with the biology of both species require seasonally specific energy expenditures (Grodzinski & Wunder, 1975; Hill, 1983; Peters, 1983) we wonder: will the carbohydrate, lipid and protein requirements of both *Peromyscus* species have a differential pattern according to the seasons and their reproductive season?

In order to know in free-living seasonal, intra- and interspecies manner the IM of *Peromyscus melanotis* and *P. difficilis* that cohabit a temperate coniferous forest of mid-latitude, in this work we describe in adult mice the seasonal behavior of indicators of the intermediary metabolism of carbohydrates (i.e., glucose), lipids (i.e., triglycerides) and proteins (i.e., urea) present in blood plasma.

2. Materials and Methods

2.1 Study Area

Desierto de los Leones National Park (PNDL; CONANP, 2006) is part of the Sierra de las Cruces, located west of the Valley of Mexico. This mountain range is a continuation of the Sierra del Ajusco. The sampling site is located at 19°18′17″ N, 99°19′14″ W, at elevations ranging from 2180 to 3200 meters. The climate is classified as temperate subhumid, type C(w2)(w′)(b′)ig (García, 2004). High temperatures occur from April to July (average = 12.6 ± 6 °C), while low temperatures are recorded from December to February (average = 8.1 ± 2 °C). Rainfall is concentrated between May and August (average = 235 ± 30 mm), and the dry season spans December to February (average = 12 ± 4 mm) (CONANP, 2006). The longest daylight hours occur from March to September (average = 12.72 ± 0.5 hrs).

Vegetation corresponds to temperate forest and is structured into the following layers (CONANP, 2006): canopy pine-fir forest (*Pinus* sp. – *Abies religiosa*) and mixed conifer-oak forest (*Pinus* sp. – *Quercus* sp.); understory includes a shrub layer (*Senecio* sp., *Salix* sp.) and a herbaceous layer (e.g., composites, rosaceae, solanaceae), with sparse grassland presence, and ground layer: characterized by abundant mosses, fungi, and some lichens growing on rocks

2.2 Specimen Collection

Adult *Peromyscus melanotis* and *P. difficilis* mice were collected monthly from March 2008 to April 2009 using Sherman traps (H. B. Sherman Traps Co., Tallahassee, FL, USA) baited with vanilla scent. Adults were identified based on body size and pelage coloration specific to each species (Álvarez-Castañeda, 2005 for *P. melanotis*, Fernández et al., for *P. difficilis*), and later confirmed *post mortem* by molar occlusal wear (Hoffmeister, 1951). On the day of capture, mice were transported to the Mammal Laboratory at UAM-I and killed for cervical dislocation, following the ethical guidelines of the DCBS Ethics Committee at UAM-I.

A pectoral incision was made to access the heart, and blood was extracted via cardiac puncture using a Pasteur pipette with anticoagulant (EDTA) to obtain the maximum volume possible. Blood samples (1.3–2 mL) were placed in Eppendorf tubes and centrifuged at 5000 rpm for 3 minutes at 25 °C (HERMLE Z-233 M-2®, Labnet International Inc., Edison, NJ, USA). Plasma was transferred to a separate Eppendorf tube and stored frozen at −5 °C until intermediary metabolism indicators were analyzed.

Each male was recorded its conventional external measurements and weight and prepared as skull and skeleton *sensu* Ramírez-Pulido et al. (1989), and incorporated as voucher specimen in the Mammal Collection of the Universidad Autónoma Metropolitana, Unidad Iztapalapa.

2.3 Blood Analysis of Metabolic Indicators

Plasma glucose, triglycerides, and urea—used as indicators of intermediary metabolism (IM) for carbohydrates, lipids, and proteins, respectively—were quantified using spectrophotometry (spectrophotometer SPECTRONIC® 20, Thermo Spectronic. Rochester, NY, USA) with commercial kits (Spinreact®), Lab-Center de México S. A. de C. V. México). All procedures followed the manufacturer's instructions.

2.4 Statistical Analysis

Data were analyzed using descriptive statistics, normality tests, homoscedasticity, and kurtosis analysis (Zar, 2007). For normally distributed data, analysis of variance (ANOVA) was used to compare seasonal intra-species variation in IM indicators. For non-normal data, Kruskal-Wallis tests were applied. Post hoc multiple comparison tests (Tukey-Kramer for parametric data and Kruskal-Wallis for non-parametric data) were used to identify significant differences (Zar, 2007). The same approach was applied to other linear variables, such as testicular weight.

Interspecific comparisons were conducted using Student's t-tests for independent samples. When normality assumptions were not met, Mann-Whitney tests were used. Linear regression analyses were performed to assess relationships between total body weight, daylight hours (DL), temperature, and IM indicators. All statistical tests were conducted at a significance level of $\alpha \leq 0.05$ using GraphPrisma® (Motulsky, 1999) and NCSS (Hintze, 2007) software packages.

3. Results

A total of 90 adult mice were collected: 25 *Peromyscus melanotis* and 65 *Peromyscus difficilis*. Table 1 presents the number of individuals per season, along with body weight and testicular weight and volume.

Table 1. *Number of adult Peromyscus mice collected by season in Desierto de los Leones National Park. Their body weight, testicular weight, and volume are indicated.*

Peromyscus melanotis	**n**	**body weight gr**	**testicles weight gr**	**testicles volumen mm³**
Spring	8	16.20 ± 2.91	0.222 ± 0.16	182.90 ± 25.40
Summer	9	17.28 ± 2.63	0.257 ± 0.16	175.10 ± 25.40
Autumn	5	15.60 ± 1.08	0.162 ± 0.12	89.22 ± 42.48
Winter	3	18.60 ± 1.91	0.305 ± 0.04	196.12 ± 54.84
Peromyscus difficilis	**n**	**body weigh gr**	**testicles weight gr**	**testicles volumen mm³**
Spring	23	37.00 ± 3.54	0.985 ± 0.18	540.30 ± 38.23
Summer	12	34.37 ± 4.74	0.616 ± 0.37	425.00 ± 55.18
Autumn	16	36.40 ± 4.53	0.590 ± 0.27	284.74 ± 47.78
Winter	14	37.54 ± 2.43	0.887 ± 0.22	515.04 ± 51.08

3.1 IIM by Season and Species

In *Peromyscus melanotis* (Fig. 1 a) glucose levels differed significantly between summer and autumn ($P < 0.0001$). Triglycerides and urea did not show significant seasonal variation. In spring, triglyceride levels were significantly higher ($P < 0.05$) than glucose and urea. During autumn and winter, both glucose and triglycerides increased ($P < 0.05$) relative to urea.

The glucose profile showed a progressive increase from spring to summer and from summer to autumn, followed by a slight decline from autumn to winter. Triglycerides tended to rise steadily from spring to winter, with a notable increase between summer and autumn. Urea levels increased from spring to summer, dropped sharply from summer to autumn, and rose again from autumn to winter.

In *Peromyscus difficilis* (Fig. 1 b) glucose levels also differed significantly between summer and autumn ($P < 0.0001$), while triglycerides and urea remained relatively stable across seasons. In spring and summer, no significant differences were observed among glucose, triglycerides, and urea. In winter, triglyceride levels were significantly higher ($P < 0.05$) than urea.

The glucose profile declined from spring to summer, rose markedly from summer to autumn, and decreased again from autumn to winter. Triglycerides dropped sharply from spring to summer, then increased through winter. Urea levels rose from spring to summer, declined from summer to autumn, and increased again in winter.

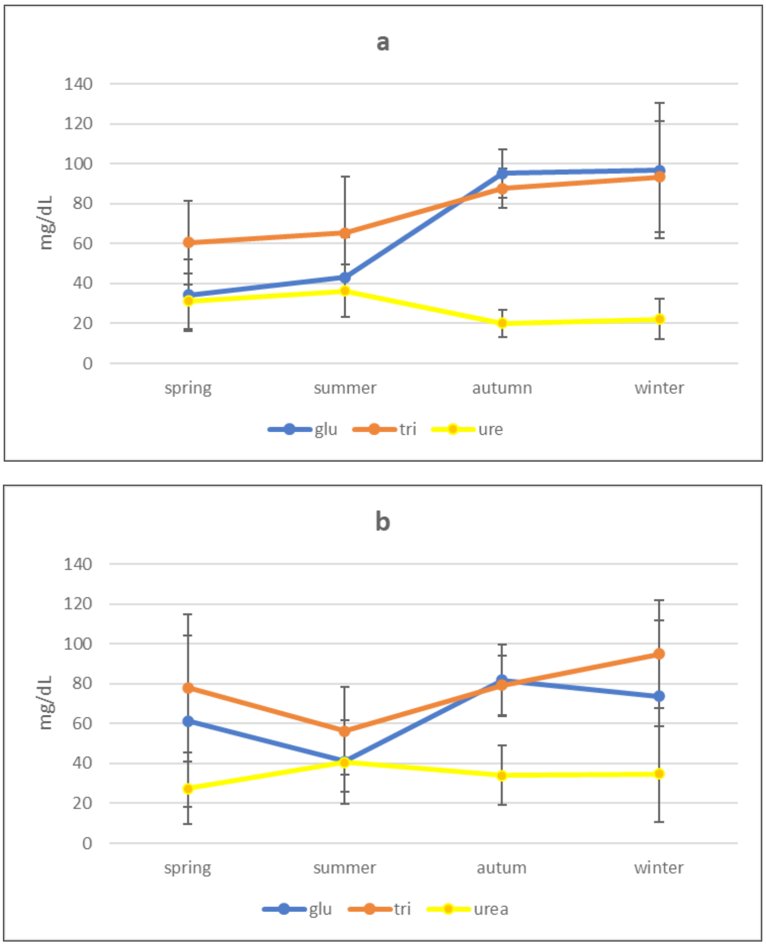

Figure 1. *Graphs showing the seasonal profile of glucose (glu), triglycerides (tri) and urea (ure) in the plasma of adult male Peromyscus melanotis (a) and Peromyscus difficilis (b) in a mid-latitude temperate coniferous forest of the Desierto de los Leones National Park, adjacent to Mexico City.*

3.2 Interspecific IIM

Although glucose, triglyceride, and urea concentrations did not differ significantly between *P. melanotis* and *P. difficilis* across seasons, each species exhibited distinct metabolic patterns (Fig. 1 a, b). For instance, from spring to summer, glucose and triglyceride levels increased in *P. melanotis* but decreased in *P. difficilis*. From autumn to winter, triglyceride levels rose more in *P. difficilis*, while glucose declined more noticeably compared to *P. melanotis*, which showed a more gradual decrease.

However, there were interspecies similarities, such as those observed in summer, autumn and winter regarding the increase in glucose and triglycerides, highlighting the urea profile which is similar between both species, in addition to the fact that the concentrations were also very similar.

3.3 Seasonal Correlations of IIM with Body Weight, Daylight Hours, and Temperature

Only statistically significant correlations ($P \leq 0.05$) are reported. In *P. melanotis* during spring, body weight was positively correlated with triglycerides

($r = 0.752$, $P < 0.031$) and negatively correlated with urea ($r = -0.766$, $P < 0.027$). Daylight hours were negatively correlated with urea ($r = -1$, $P < 0.011$).

In *P. difficilis* during summer, temperature was positively correlated with glucose ($r = 0.634$, $P < 0.027$), while body weight was negatively correlated with triglycerides ($r = -0.559$, $P < 0.059$). During winter, daylight hours were positively correlated with triglycerides ($r = 0.999$, $P < 0.032$).

4. Discussion

Wild rodents living freely in natural habitats play a relevant role in their ecosystems, acting as dispersers of seeds and arboreal mycorrhizae, soil modifiers, and contributors to various ecological processes (Forget & Milleron, 1991; Mangan & Adler, 2002). Like all animal species, they require nutritional input for growth and development. Nutritional demands depend on species-specific factors (e.g., growth rate, age, lifespan, body size, reproductive cycles), as well as environmental pressures related to their distribution range (e.g., climate, physiography, habitat conservation status).

Metabolic studies in wild rodents have employed various techniques, including heart rate telemetry (e.g., Grodzinski & Wunder, 1975) and the doubly labeled water method (deuterium isotope – $D_2{}^{18}O$ –) (e.g., Mullen, 1971; Randolph, 1980; Corp et al., 1999). Each method has its advantages and limitations when applied to field conditions (see Butler et al., 2004).

Within the genus *Peromyscus*, research on metabolism and energy requirements has primarily focused on northern populations (i.e., Canada and the USA), particularly *P. maniculatus* and *P. leucopus*. Fleharty et al. (1973) examined body composition, energy content, and lipid cycles in four rodent species from Ellis County, Kansas, and found distinct lipid cycles, considered direct indicators of energy reserves. For instance, *P. maniculatus* exhibited elevated energy demands during winter.

Other studies from northern U.S. regions (Sealander, 1951; Hayward, 1965; Sawicka-Kapusta, 1968; Lynch, 1973), characterized by extreme climates and low winter temperatures, reported similar patterns of lipid accumulation, suggesting that fat serves both as insulation and a metabolic energy source during colder months.

In contrast, data from southern regions with temperate climates and more stable microhabitats reveal different trends. Rodent populations in these areas show significant fat reductions during reproductive periods (Caldwell & Connell, 1968; Fehrenbacher & Fleharty, 1976). Judd et al. (1978) linked lipid cycles to reproductive parameters in *P. leucopus* from the Rio Grande Valley, Texas, finding lower fat levels during peak reproductive activity.

Derting & Hornung (2003) investigated seasonal changes in digestive organ size in *P. leucopus* from western Kentucky, where moderate winters and humid summers influenced organ mass and function. Vázquez et al. (2004) studied *P. aztecus* and *R. fulvescens* in pine-oak forests of west-central Mexico, analyzing stomach and fecal contents and evaluating macronutrient (e.g., lipids) composition of consumed plants.

Collectively, these studies clarify the relationship between diet and energy demand under varying environmental and reproductive conditions in *Peromyscus*. However, they do not provide direct insights into metabolism in free-living individuals.

Daily macronutrient intake—measurable in biological samples such as blood—is reflected in intermediary metabolism indicators (IIMs). IIMs offer a snapshot of an animal's nutritional status based on compound concentrations (e.g., Lee et al., 1978; Bavera, 2000). Glucose is commonly used to assess carbohydrate metabolism; triglycerides for lipid reserves; and urea for protein catabolism, as it reflects nitrogen derived from protein intake.

The spatial and temporal assessment of IIMs in free-living rodents began with *P. melanocarpus* populations in a montane cloud forest in the Sierra Madre of Oaxaca, Mexico (Arturo Salame-Méndez, Mireya Valdez-Gómez & Miguel Briones-Salas – Valdez-Gómez, 2009 –). Seasonal comparisons across age categories and sex in disturbed and undisturbed sites revealed no significant differences in IIMs.

The feeding habits of *Peromyscus melanotis* and *P. difficilis* populations in the study areas comprised of temperate coniferous forests have been described. Both species are omnivorous, with the majority of their diet consisting of plant matter, including nectar, soft and hard plant parts, seeds, insects, and they also consume fungi during the rainy season (e.g., Alondra Castro-Campillo & Claudia Peralta-Juárez – Peralta-Juárez, 2015 –). Thus, the set of spatial and temporal dietary items of both species in the study areas provide them with the energy inputs necessary to cover their energy expenditure during their ontogeny, in addition to having phytochemicals that could regulate their reproductive physiology (e.g., phytoestrogens and mycoestrogens – Salame-Méndez et al., 2020 –), as well as others that could regulate other physiological processes. For example, during dry and cold seasons, when seed consumption by mice of both species increases, in addition to being rich in fats and fatty acids, the plants consumed during this time must contain hyperlipidemic, antioxidant, and orexigenic phytochemicals (e.g., Elshafie et al., 2023) that together would allow the mice to withstand the physiological stress caused by inclement weather during autumn and winter.

Previous work has shown that temporal fluctuations in *Peromyscus melanotis* population density during the fall-winter environmental conditions in the study area are very low or non-existent. We therefore infer that the species is very sensitive to environmental changes and is therefore less active when humidity and temperatures are lower (Castro-Campillo et al., 2008). However, although *P. melanotis* is less active at low temperatures due to its likely low IM, it tends to increase; this is supported by the increase in plasma glucose and triglycerides compared to spring and summer, respectively. Therefore, in *P. melanotis*, by increasing its IM during autumn-winter, its movement energy remains without significant changes, which allows it to segregate spatio-temporally in the use of the microhabitat with its congener *Peromyscus difficilis*, which is a passive species, and of larger size and weight (De- La-Cruz et al., 2019, 2020, 2021).

In adult male mice, since they are primarily responsible for reproductive activity, they must have a high energy expenditure during this period. Therefore, their high energy expenditure must be compensated by the type of food and the catabolism of fats - e.g. triglycerides - by lipolysis and β-oxidation of fatty acids, as well as by glycolysis, contained in their food. Thus, in adult males of *Peromyscus melanotis* and *Peromyscus difficilis*, it was expected that during their greatest reproductive activity both the concentrations of glucose and triglycerides would be elevated, but this only occurred in one of the species, and in both species, the body weight of adult males did not decrease significantly (Table 1).

In adult male *Peromyscus melanotis*, plasma glucose and triglyceride levels increased in the summer, a time when reproductive activity and exploratory activity are the highest. In *Peromyscus difficilis*, which also reproduces year-round but peaks in reproductive activity in spring, plasma glucose and triglyceride levels decreased.

The increase in glucose and triglycerides in *Peromyscus melanotis* during the summer, when their reproductive activity peaks, indicates that even when these IIMs increase, their utilization is scarce. In *Peromyscus difficilis*, the decrease in both metabolic indicators during the spring is due to their greater catabolism, thus compensating for the energy expenditure caused by reproductive activity. However, in adult males of both species, glucose concentrations are low in feces (results not shown), indicating a greater bioenergetic use of glucose. Therefore, even when there is an interspecies difference in circulating glucose and triglyceride contents during reproductive activity, when there is greater energy expenditure, this is compensated by a high rate of glucose catabolism.

In adult males of both *Peromyscus* species, circulating levels of glucose and triglycerides increase during the dry and cold winter season—indicating greater uptake and potential utilization of fast energy from carbohydrates (IIM: glucose) and stored energy in the lipids (IIM: triglycerides), in addition to the fact that both IIMs are scarce eliminated in feces (results not shown). Therefore, during autumn and winter, fats provide protection against low temperatures, and their catabolism, along with glycolysis, maintains your body temperature. The aforementioned would contribute to reproduction and therefore this process would not cease but only decrease during dry seasons and with low temperatures as has been demonstrated endocrinely (Salame-Méndez et al., 2004, 2008).

Regarding environmental factors in the study area, such as daylight hours and temperature, that could be seasonally related to IIM, the following is indicated. Although some correlations showed a medium to high, either positive or negative, and significant r (e.g., in *P. difficilis*, daylight hours-winter had a high and positive correlation with triglycerides), in general, the correlations were medium to high, positive or negative, but not significant, indicating limited reliability. Therefore, we cannot conclusively attribute seasonal IIM variation to these environmental factors in both species.

5. Conclusion

In adult males of *Peromyscus melanotis* and *Peromyscus difficilis* in the study area, regardless of body size, the seasonal profiles of glucose, triglycerides, and urea are generally similar, and are particularly different during the seasons of greatest reproductive activity. Therefore, starting in spring and continuing through summer, the increase in temperature, associated with visible light, humidity, and increased forest productivity, allows both species to meet the high energy burden of reproduction through the catabolism of fats and sugars.

The strategy followed by both *Peromyscus* species to avoid competition is to have asynchronous reproductive cycles even though they reproduce year-round. Therefore, *Peromyscus difficilis* reproduces mainly in spring and *P. melanotis* during the summer. Meanwhile, environmental factors (daylight hours and temperature) could seasonally affect IIM and therefore intermediary metabolism. In this sense, what happens during the dry and cold winter season on the IIM of carbohydrates and lipids in both species, although both environmental factors did not have a significant effect on glucose, triglyceride, and urea contents, cannot be ruled out. However, it should also be considered that the plant items consumed by mice of both species must contain phytochemicals, for example, with orexigenic activity and others that stimulate triglyceride increases. Thus, environmental factors and phytochemicals in dietary ingredients together regulate the physiology of body weight gain in mice during the dry and cold seasons. This provides a metabolic explanation that complements the endocrine evidence (e.g., androgen production) as to why adult males (like other age categories) that make up the populations of both *Peromyscus* species studied during the fall and into the late winter period see their reproductive activity not cease but only decrease.

Finally, assessing spatiotemporal IIMs provides simple, reliable, and low-cost information on the metabolism of individuals in the species under study. This provides another tool for understanding the energy needs of species using an ecophysiological approach and can complement diet studies.

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