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Diet effects on ectotherm thermal performance

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ABSTRACT

The environment is changing rapidly, and considerable research is aimed at understanding the capacity of organisms to respond. Changes in environmental temperature are particularly concerning as most animals are ectothermic, with temperature considered a key factor governing their ecology, biogeography, behaviour and physiology. The ability of ectotherms to persist in an increasingly warm, variable, and unpredictable future will depend on their nutritional status. Nutritional resources (e.g. food availability, quality, options) vary across space and time and in response to environmental change, but animals also have the capacity to alter how much they eat and what they eat, which may help them improve their performance under climate change. In this review, we discuss the state of knowledge in the intersection between animal nutrition and temperature. We take a mechanistic approach to describe nutrients (i.e. broad macronutrients, specific lipids, and micronutrients) that may impact thermal performance and discuss what is currently known about their role in ectotherm thermal plasticity, thermoregulatory behaviour, diet preference, and thermal tolerance. We finish by describing how this topic can inform ectotherm biogeography, behaviour, and aquaculture research.

Key words: nutrition, thermal biology, plasticity, ectotherm, microbiome, lipid, macronutrient, thermal tolerance, thermal limit.

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I. INTRODUCTION: ECTOTHERM DIETS CAN CHANGE WITH TEMPERATURE

Global climate change is reshaping ectotherm nutrition by altering food availability, food options, prey quality, inter- and intraspecific interactions, foraging success, and diet selection (Fig. 1; Birnie-Gauvin *et al.*, 2017; Cross *et al.*, 2015; Hallam & Harris, 2023; Pörtner *et al.*, 2019; Rosenblatt & Schmitz, 2016; Zhang *et al.*, 2020; Huey & Kingsolver, 2019). While multiple factors influence how nutritional resources vary spatially and temporally, temperature can act directly on ectotherm nutrition by inducing changes in prey abundance (both increases or decreases) and altering food options and prey quality (Alton *et al.*, 2020; Arnold *et al.*, 2010; Birnie-Gauvin *et al.*, 2017; Ho, Pennings & Carefoot, 2010). For example, marine heatwaves in the North American Pacific between 2014 and 2016 are implicated as the drivers of a wasting disease outbreak that decimated populations of multiple sea star species and canopy-forming kelp species in several regions (Beas-Luna *et al.*, 2020; Cavole *et al.*, 2016). Extreme events like this can have lasting impacts on community composition and lead to species invasions or range shifts, thus, altering available food options (Cavole *et al.*, 2016; Michaud, Reed & Miller, 2022). Similar changes are occurring in tropical systems, where increasing temperatures, extreme weather events, overfishing, and invasive species can shift reefs from coral dominated to algae dominated, impacting resource availability throughout the ecosystem

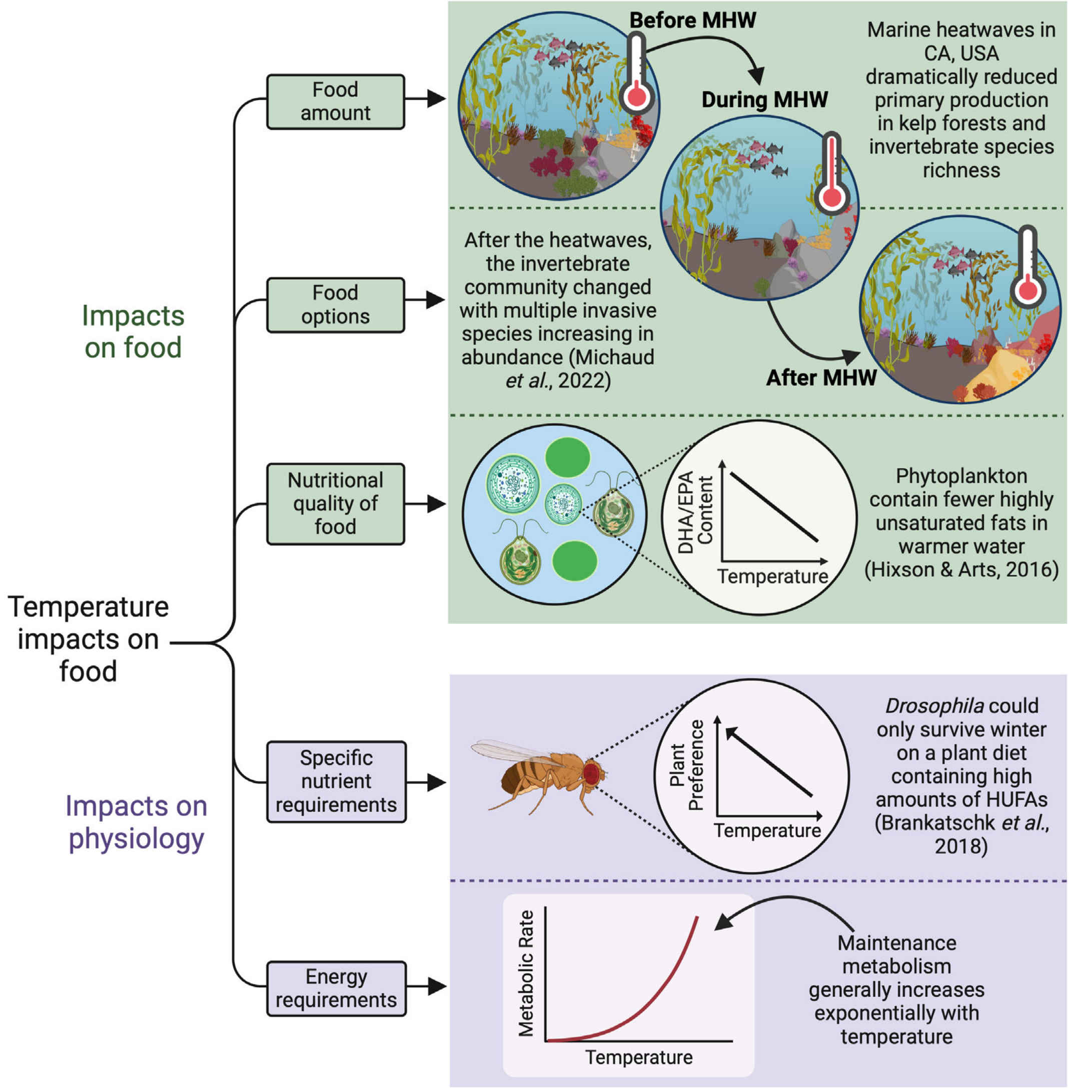

Fig. 1. Conceptual figure illustrating ways in which temperature can influence ectothermic animal nutrition and examples of each scenario. Temperature may impact ectotherm nutrition by directly impacting food resources (e.g. availability, options, quality) or by affecting the nutritional requirements of the animal (e.g. specific nutrient requirements, energy requirements). Importantly, in many cases, animals can respond to changes in their food landscape or nutritional needs by adjusting how, when, and on what they forage and consume. This can occur through changes in the total amount they consume or their diet selection. HUFA, highly unsaturated fatty acid; MHW, marine heatwave. Created with biorender.com.

(Burkepile & Hay, 2008). Other human impacts may also affect food availability in correlation with changes in temperature. For example, introductions of mosquitofish in California, USA have caused dramatic declines in wetland zooplankton and macroinvertebrates, at the same time as the region has experienced severe drought and warming (Preston *et al.*, 2017). Such changes are also occurring in terrestrial systems, where warming is associated with shifts in species abundance across tundra, grassland, and high-latitude ecosystems (Grimm *et al.*, 2013).

The nutritional quality of a diet item can also change with temperature (Fig. 1). For example, the global availability of the omega-3 fatty acids, docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), which are almost exclusively made by aquatic primary producers, is expected to decline with increasing temperatures due to climate change (Hixson & Arts, 2016; see Section III.2). Warming may also affect dietary fat content, as illustrated by Tseng *et al.* (2021), where algae raised in warmer water contained a lower amount of neutral lipids. In terrestrial plants, environmental temperature and CO_2 levels influence the carbohydrate and protein content of multiple species (Rosenblatt & Schmitz, 2016). Changes in nutritional quality are not limited to primary producers. For example, warming was associated with higher cholesterol content in copepods (Hassett & Crockett, 2009), and a lower carbon to phosphorus ratio in water fleas (*Daphnia* sp.) (Prater, Wagner & Frost, 2018). While some of these predictions apply at a global scale, many temperature-induced shifts in nutrition are species or location-specific. Given the dynamic nature of food webs under changing temperatures, there is a clear need to understand the consequences of these changes on ectotherm thermal physiology and behaviour.

While temperature can directly impact the nutritional landscape for animals, it also can affect their nutrient requirements (Fig. 1), i.e. their energetic or specific nutrient requirements. Importantly, some ectotherms adjust their diet preference and/or selection to meet their nutritional needs and thereby compensate for changes in available food resources (Boersma *et al.*, 2016; Carreira *et al.*, 2016; Jang *et al.*, 2015; Rho & Lee, 2017; Schmitz & Rosenblatt, 2017; Vejříková *et al.*, 2016). Temperature may also impact diet selection by altering the animal's inter- and intraspecific interactions through mismatches in the timing of consumer and food abundance or through behavioural changes, such as willingness to perform risk-taking behaviours or disruption in sensory detection of food (Draper & Weissburg, 2019; Hallam & Harris, 2023; Rosenblatt & Schmitz, 2016; Schmitz & Rosenblatt, 2017). Researchers have also explored the temperature dependence of specific nutrient requirements in some ectotherms. Interestingly, some species prefer diets rich in carbohydrates relative to protein under warmer conditions (Lee *et al.*, 2015; Rho & Lee, 2017; see Section III.1) and some omnivorous ectotherms adjust the proportion of plant to animal prey in their diet with temperature (Zhang *et al.*, 2020; Brankatschk *et al.*, 2018; see Section III.2). While research has demonstrated that animal diets can change in correlation with or directly in response to temperature, the impacts of these diet changes on ectotherm biology are not well understood. Organismal level consequences (both lethal and sublethal, Fig. 2) could scale to population-, species-, and ecosystem-level effects with important conservation implications.

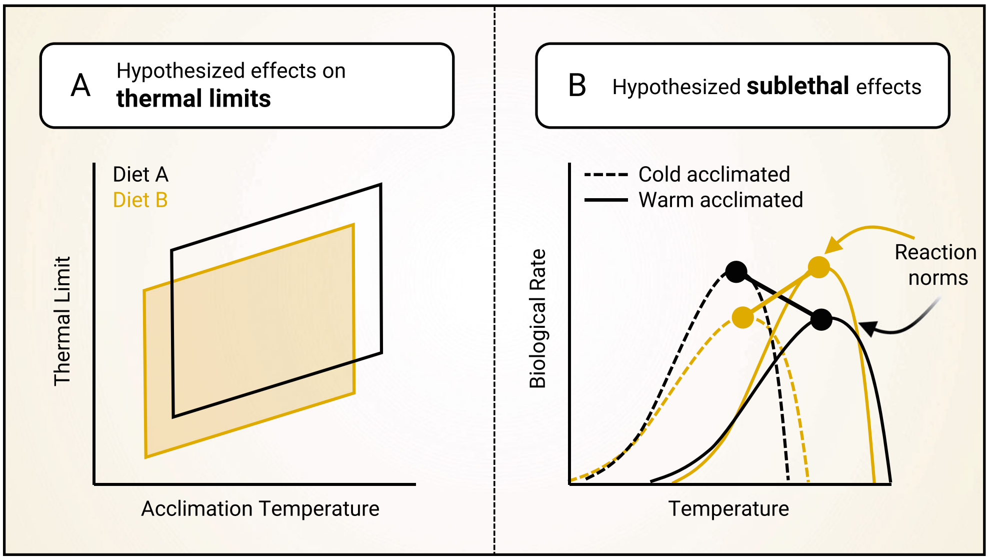

Fig. 2. Hypothesised ways in which diet may influence thermal limits (A) or biological rates (B) in ectotherms. (A) Diet may increase or decrease cold and warm thermal limits, thereby changing the 'zone of resistance' or range of temperatures ectotherms can survive at for brief periods of time (Fry, 1971; Hofmann & Todgham, 2010). (B) Diet could impact ectotherms sub-lethally by affecting the height, width or shape of acute thermal performance curves for biological rate processes (e.g. growth, locomotion, reproduction, heart rate, digestion).

II. PHYSIOLOGICAL CONSEQUENCES OF CHANGES IN DIET WITH TEMPERATURE

Researchers characterise the thermal biology of ectotherms by measuring their (*i*) tolerance to extreme temperatures or thermal limits, and (*ii*) performance across a thermal gradient (Figs 2 and 3). Diet and temperature can influence both thermal limits and biological rates, including growth, metabolism, cardiac function, locomotion, digestion and more (e.g. Hardison *et al*., 2021; Papadopoulou *et al*., 2022; Hardison, Schwieterman & Eliason, 2023; Brankatschk *et al*., 2018; Lee *et al*., 2015; Rho & Lee, 2017; Clissold, Coggan & Simpson, 2013).

(1) Thermal limits

Thermal limit tests are rapid assessments of thermal tolerance that can be used to compare resilience to extreme temperatures across species, populations, environments, and treatments. Since their introduction in the 1940s, researchers have conducted thousands of thermal limit tests across diverse taxa, revealing global scale patterns that have aided researchers and managers in identifying species, environments, and populations most at risk under global climate change (Brett, 1944; Fry, Brett & Clawson, 1942; Fry, 1957; Deutsch *et al*., 2008; Hofmann & Todgham, 2010; Somero, 2010; Sunday *et al*., 2014, 2019). Diet can impact both upper and lower thermal limits, indicating that it is an underappreciated but important factor determining the range of temperatures that can be tolerated during acute heat stress (Abdel-Ghany *et al*., 2019; Craig, Neil & Gatlin, 1995; Gomez Isaza *et al*., 2019; Gupta *et al*., 2010; Tejpal *et al*., 2014; Dixon *et al*., 2023; Papadopoulou *et al*., 2022).

During thermal limit tests, animals are rapidly warmed or cooled until a pre-defined endpoint (e.g. inability to right oneself or loss of equilibrium, cardiac arrhythmia, lethal temperature) is reached. Diet has been shown to alter thermal limits across several different methods (Fig. 3). For example, dietary lipid composition modified lower critical thermal limits (CT_{min}; endpoint = loss of equilibrium) and lethal temperatures in the fishes red drum (*Sciaenops ocellatus*; Craig *et al*., 1995) and Nile tilapia (*Oreochromis niloticus*; Abdel-Ghany *et al*., 2019) fed pelleted diets containing different oil types. In both cases, pellets with higher levels of oil rich in highly unsaturated fatty acids conferred better cold tolerance. Highly unsaturated fats are associated with greater membrane fluidity, while

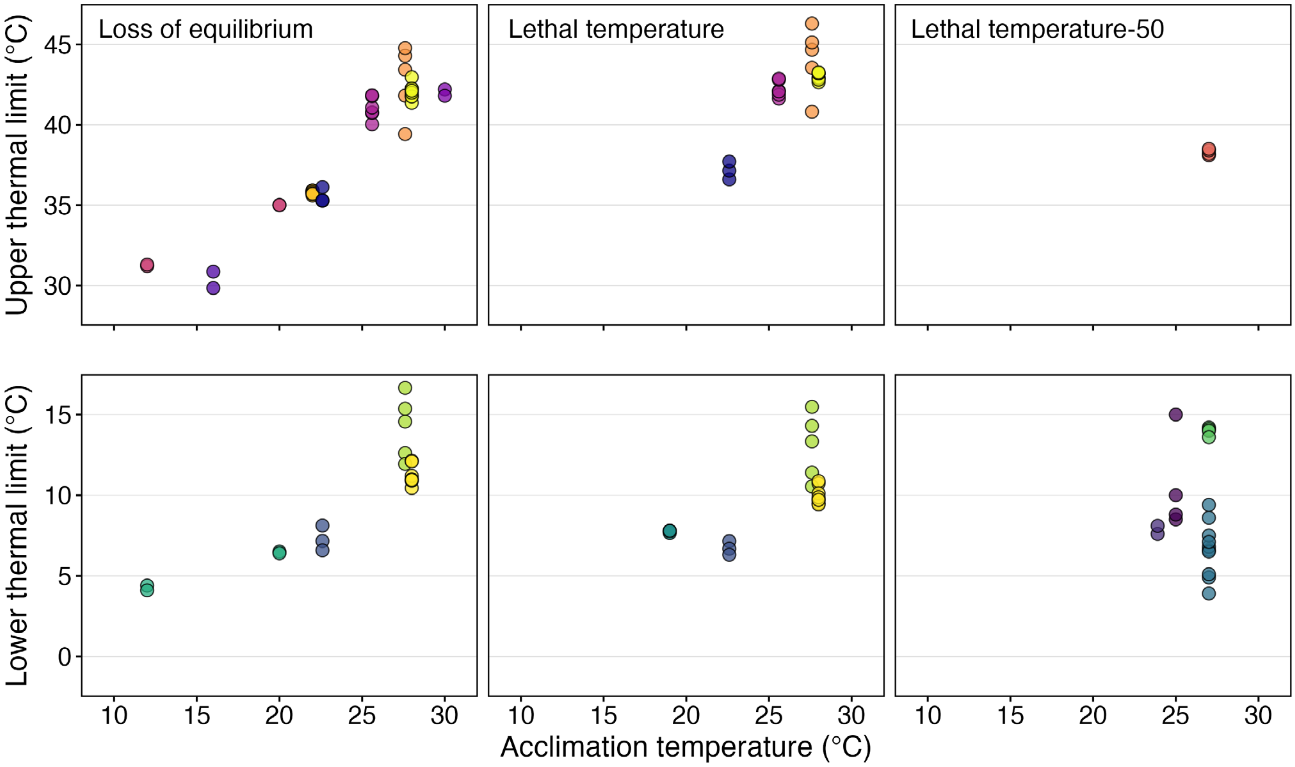

Fig. 3. Thermal limit data from 13 fish studies where more than one diet treatment was used and thermal tolerance was assessed using standardised methodology (see online Supporting Information, Table S1, for data sources). The top panels are data from studies that measured upper thermal limits (i.e. warm tolerance) and the bottom panels are data from studies that measured lower thermal limits (i.e. cold tolerance). Data are plotted separately according to the test method used to estimate thermal limits: loss of equilibrium, lethal temperature test, or lethal temperature where 50% of individuals perished (Lethal temperature-50). Colours indicate specific studies and individual points represent different diet treatments used in that study.

saturated fats are associated with higher membrane stability. This suggests that dietary lipid composition can alter membrane thermal performance; a mechanism discussed in detail in Section III.2.

Other studies have revealed that dietary supplementation of specific micronutrients, including L-tryptophan (amino acid), levan, and dietary *β*-alanine (decreases cardiomyocyte taurine uptake) can alter upper thermal limits (Gupta *et al*., 2010; Tejpal *et al*., 2014; Dixon *et al*., 2023). Nevertheless, this does not always appear to be the case (see Hardison *et al*., 2021; Ikeda *et al*., 2011; Atwood *et al*., 2003). Given the multiple potential mechanisms by which diet may alter thermal limits (see Section III), it is critical that we integrate diet effects into our understanding of thermal limits in wild and farmed ectotherms. It may be the case that we have overestimated the thermal breadth of ectotherms living in altered or resource-poor environments or underestimated it for ectotherms with high-quality or more flexible diets in the wild compared to the controlled laboratory conditions under which they are most often studied (Figs 2 and 3).

(2) Sublethal effects of diet and temperature

While thermal limits define the extreme temperatures that ectotherms can survive in for short periods of time, they do not capture sublethal effects of temperature on ectotherm biology. Thermal limits and maximum rate capacities are considered less plastic than performance traits such as resting and standard metabolic rate, growth, consumption, etc.; a hypothesis termed ‘plastic floors and concrete ceilings’ (Araujo *et al*., 2013; Hoffmann & Sgrò, 2011; Sandblom *et al*., 2016). These traits provide greater insights into how population growth, species interactions, and behaviour shift with temperature.

Biological rates typically increase with acute warming until they reach a peak, after which they rapidly decline, resulting in a classic acute thermal performance curve (TPC) (Fig. 2B). Importantly, TPCs are plastic, and can change in height, width or shape after thermal acclimation (Schulte, Healy & Fangue, 2011; Fig. 2B). TPCs provide valuable data that can be used to inform models and management efforts for ectotherms. However, there are several limitations involved in extrapolating individual performance curves to larger ecological processes, including that factors like diet, which are often not considered, can alter the shape of TPCs throughout the time course of acclimation (Carreira *et al*., 2020; Hardison *et al*., 2021, 2023; Huey & Buckley, 2022, Sinclair *et al*., 2016, Fig. 2B). In addition, different performance traits can be characterised by different TPCs (Clark, Sandblom & Jutfelt, 2013), potentially creating trade-offs if a diet maximises the performance of one trait at the cost of maintaining high performance in another (Hardison *et al*., 2021). While certainly complex, we can improve our predictions for how diet affects ectotherm thermal performance by considering the physiological mechanisms by which diet alters thermal physiology.

III. MECHANISMS OF INTERACTION BETWEEN DIET AND TEMPERATURE ON ECTOTHERM PHYSIOLOGY

(1) Macronutrient ratios

As temperature increases, so does baseline metabolism. To meet this rising metabolic demand, ectotherms must take in more fuel. One way to accomplish this is by increasing food intake rate, which has been demonstrated in many ectotherms across their optimal thermal range (Jutfelt *et al*., 2021). Interestingly, many ectotherms also change their preferred macronutrient ratios, in addition to consumption rates, with temperature (Devries & Appel, 2014; Lee *et al*., 2015; Rho & Lee, 2017; Schmitz, Rosenblatt & Smylie, 2016).

The macronutrient ratio hypothesis (MRH) is a proposed explanation for why ectotherms alter macronutrient preferences with temperature. The MRH suggests that the preferred protein to carbohydrate ratio will decrease as temperature increases (Devries & Appel, 2014; Lee *et al*., 2015; Lemoine & Shantz, 2016; Schmitz *et al*., 2016; Rho & Lee, 2017; Rowe *et al*., 2018), due to a trade-off between high protein (maximising growth) and high carbohydrate (maximising energy gain). The MRH proposes that as metabolic demand increases with temperature, ectotherms will require a greater proportion of easy-to-digest energy sources. Carbohydrates can be digested more efficiently in warm conditions relative to protein because protein is not readily stored as fuel in the body and contains nitrogen, which must be either assimilated or excreted as waste whereas carbohydrates can easily be stored as glycogen and do not contain nitrogen (Lee *et al*., 2015; Rho & Lee, 2017).

Some studies have found support for the MRH. For example, Lee *et al*. (2015) tested the effect of variable protein to carbohydrate ratios in caterpillar (*Spodoptera litura*) diets across three temperatures (20 °C, 25 °C, and 30 °C). The researchers compared performance under fixed-ratio diets to a choice diet and found that the caterpillar’s preference for carbohydrates increased with warming and that across the tested temperatures the choice diet generally maximised performance (quantified as development time and pupal mass). An alternative to the MRH is that higher-protein diets will be preferred as temperatures increase to maintain maximal growth and protein turnover in response to an individual’s rising metabolic demands (Devries & Appel, 2014; Lemoine & Shantz, 2016; Schmitz *et al*., 2016; Rowe *et al*., 2018). In support of this hypothesis, Schmitz *et al*. (2016) found that juvenile grasshoppers (*Melanoplus femurrubrum*) ate more protein relative to carbohydrates at hotter temperatures in predator-exposed and risk-free treatments. Similarly, Devries & Appel (2014) found that silverfish (*Lepisma saccharina*; a primitive wingless insect) preferred proportionally higher amounts of protein and lipid relative to carbohydrates in their diet as temperature increased.

Recent studies have proposed a derivative of the MRH, called the temperature metabolic stoichiometry (TMS) hypothesis, which again argues that ectotherms will preferentially consume higher carbon diets (relative to nitrogen and phosphorus) due to their rising metabolic demands (at the direct cost of growth) as temperature increases (Boersma *et al.*, 2016; Malzahn, Doerfler & Boersma, 2016; Zhang *et al.*, 2020). However, empirical evidence for this hypothesis is limited (Boersma *et al.*, 2016; Malzahn *et al.*, 2016). Anderson *et al.* (2017) used a modelling approach to test the TMS hypothesis and found no evidence that zooplankton diets will shift to a higher carbon to nitrogen ratio with warming. They noted that previous stoichiometric models assumed that consumption rates would not change with temperature; when their model did not include changes in consumption with temperature, it supported the TMS hypothesis, but when temperature effects on consumption rates were incorporated, the model predicted no change in the optimal carbon to nitrogen ratio with temperature. Importantly, Anderson *et al.* (2017) did show that ectotherms require more carbon as temperature increases, but that this could be met through higher consumption rates in warmer conditions rather than changes in the preferred stoichiometric ratio. For additional reading, Cross *et al.* (2015) used ecological stoichiometry and metabolic theory to examine how interactions of stoichiometry and temperature on an individual level may scale to whole-ecosystem effects.

Ruiz *et al.* (2020) expanded on the TMS hypothesis, contending that stoichiometric preferences will follow a U-shaped response curve with lower carbon to phosphorus ratios (corresponding to higher growth) being advantageous at optimal temperatures for growth. Outside the optimal thermal range for growth, the need to consume a greater proportion of carbon relative to phosphorus increases. Ruiz *et al.* (2020) found support for a U-shaped response using modelling and experimental work on *Daphnia* sp. Other traits may also have performance trade-offs in response to different dietary protein to carbohydrate ratios. Using a nutritional geometry framework, Kutz, Sgrò & Mirth (2019) demonstrated that developmental temperature interacted with dietary protein to carbohydrate ratio in trait-specific ways in larval fruit flies (*Drosophila melanogaster*). They used 36 diets that varied in protein and carbohydrate content as well as energy density and then measured development time, viability, and adult size and morphology after acclimation to the treatment diets at 25 °C or 28 °C. At the current summer temperature (25 °C), fly performance was optimal across a wide nutritional space. However, when flies were reared under a higher temperature (28 °C; climate-change scenario), there were fewer dietary options that maximised fly performance. These results suggest that suboptimal temperatures may limit the dietary options capable of maximising an animal's performance. Similarly, cold-acclimated *Daphnia* sp. showed a wide flattened growth curve across a range of carbon to phosphorus ratios in their diet (Laspoumaderes *et al.*, 2022). However, when warm acclimated, growth was maximal across a smaller number of diets (Laspoumaderes *et al.*, 2022). The authors contend that the optimal ratio of carbon to phosphorus depends on the thermal sensitivity of metabolic rate, growth, and ingestion, where a higher carbon to phosphorus ratio is required when an animal's thermal sensitivity for metabolism exceeds that of ingestion or growth (Laspoumaderes *et al.*, 2022). A similar nutritional framework was used in Rowe *et al.* (2018) to determine how the dietary protein to carbohydrate ratio impacted resting and active metabolic rate in damselfish (*Abudefduf vaigiensis*). The damselfish's macronutrient selection changed in response to temperature and the macronutrients that were offered to them during feeding trials (Rowe *et al.*, 2018). While the nutritional geometry framework used in these studies is experimentally challenging due to the large number of treatments, it provides a more complete picture of how nutrition and temperature may interact and allows for determination of complex and multi-optima nutritional effects.

There are several noteworthy limitations to the MRH and TMS hypotheses. Firstly, most studies have been conducted on larval or juvenile ectotherms. Growth rates change across life history, so the costs and benefits of higher growth compared to higher energy yielding diets may differ with age. Second, the MRH focuses on the dietary protein to carbohydrate ratio but does not include the lipid component of the diet, which is also undoubtedly important, especially in marine environments where lipids are a more bioavailable energy source than carbohydrates and some aquatic animals have low glucose tolerance (Steinberg, 2022; Turchini *et al.*, 2022).

A third limitation is that these hypotheses do not account for variation in nitrogen excretion across taxa. Protein is the only metabolizable macronutrient class that contains nitrogen. This nitrogen is released as ammonia during protein catabolism which becomes toxic if left to accumulate and must be excreted or converted to less toxic compounds (e.g. uric acid, urea). Ammonia production is directly related to the amount of protein catabolised (Randall & Wright, 1987). Consequently, ectotherms consuming high-protein diets excrete more nitrogen than those consuming low-protein diets. Most terrestrial animals are either ureotelic (excrete urea) or uricotelic (excrete uric acid), while many aquatic organisms are ammoniotelic (excrete ammonia). The production and excretion of urea and uric acid are more energetically demanding than the excretion of ammonia (Randall & Wright, 1987). Additionally, nitrogen excretion rate generally increases with temperature due to rising metabolic rates. Thus, differences in nitrogen waste removal may reduce the cost of consuming high-protein diets at high temperatures in ammoniotelic animals, which could explain some of the observed differences in macronutrient selection across taxa.

(2) Lipids

Lipid quality can impact thermal limits and other sublethal thermal performance traits in ectotherms (Abdel-Ghany *et al.*, 2019; Craig *et al.*, 1995; Geiser, Firth & Seymour, 1992; Hassett & Crockett, 2009; Hoar & Cottle, 1952). Lipids play a key role in cell membranes, cell signalling, gene regulation, energetics, and other processes. Lipids vary tremendously in their thermal properties. As rising temperatures increase the fluidity and can alter the phase state of membranes, ectotherms modify their membrane composition to maintain its function across temperatures (Hazel, 1995; Hochachka & Somero, 2002). This can involve multiple mechanisms, including remodelling of the cell membranes by exchanging phospholipids and sphingolipids for those with different headgroups or acyl chains, inserting cholesterol or altering membrane-bound protein concentrations (Hochachka & Somero, 2002). A common mechanism of homeoviscous adaptation (i.e. the process of optimising membrane fluidity in response to temperature) is to adjust the composition of fatty acids in the membrane. As fatty acid tail length and degree of saturation increases, so does the interaction strength (due to van der Waals forces) between acyl chains in membranes (Hochachka & Somero, 2002). This suggests that longer and more saturated fatty acids in the diet should decrease membrane fluidity, while unsaturated fatty acids and fatty acids with short acyl chains in the diet increase membrane fluidity (Hochachka & Somero, 2002).

There is evidence to support the hypothesis that dietary fat composition can influence thermal performance in ways predicted by homeoviscous adaptation. For example, Hardison *et al.* (2023) found that opaleye fish (*Girella nigricans*) acclimated to 12 °C or 20 °C and fed brine shrimp, algae or both, assimilated different fatty acids into their heart tissue. Fish with more ventricular unsaturated fats had greater maximum heart rates (i.e. improved performance) under cold acclimation, but lower maximum heart rates under warm acclimation (Hardison *et al.*, 2023). Brankatschk *et al.* (2018) found evidence for an influence of dietary fat composition on thermal performance in *D. melanogaster*. Interestingly, the flies preferred plants high in unsaturated fats as food, compared to yeast (low in unsaturated fats), at cold 'winter' temperatures (12 °C). Plant consumption was associated with higher cold tolerance (e.g. greater mobility, higher overwinter survival) and greater tissue polyunsaturated fatty acid content. Thus, the flies appeared to choose their diet based on fatty acid composition in ways that maximised overwinter survival. These results are consistent with those from other overwintering insects where increased unsaturated fatty acid composition in winter is argued to support functional membrane composition as well as lipid metabolism (Sinclair & Marshall, 2018), and with studies that measured the effects of dietary lipid composition on thermal limits (see Section II.1). It would be interesting to investigate whether dietary generalist species have a wider thermal breadth than specialists with more constrained diets. Further, dietary adjustments to assimilate different lipids with temperature changes may be most important in ectotherms living in environments that experience extreme daily or seasonal temperatures.

It can be energetically expensive to alter the length or degree of saturation of fatty acids or synthesise lipids *de novo* (Secor, 2009), and many animals cannot synthesise certain lipids and must assimilate them from their diet [for a review in fish, see Turchini *et al.* (2022) and in insects, see Sinclair & Marshall (2018)]. Thus, ectotherm tissue lipid composition often differs depending on dietary lipid composition, at least for essential lipids and others that are expensive to synthesise (Alhazzaa *et al.*, 2013; Atwood *et al.*, 2003; Craig *et al.*, 1995; Farkas *et al.*, 1980; House, Riordan & Barlow, 1958; Vagner *et al.*, 2019). However, animals are also capable of lipid regulation and tissues can be differentially affected by dietary lipid deficiencies. For instance, Skalli *et al.* (2006) found that dietary deficiency of certain essential fatty acids had a greater impact on the fatty acid content of muscle, liver, and gills than that of eye and brain tissue in juvenile European sea bass (*Dicentrarchus labrax*). While many ectotherms have some capacity to alter acyl chains through desaturase or elongation activity or to prioritise lipid deposition in specific tissues, there is still a strong energetic incentive for ectotherms to alter their diet strategy if they are placed in temperatures where their current diet has a sub-optimal lipid profile (Brankatschk *et al.*, 2018). An energetic trade-off between synthesis and assimilation of lipids can affect growth rate. For example, dietary deficiency of omega-3 fatty acids in Atlantic salmon (*Salmo salmar*) resulted in higher bioaccumulation of DHA [i.e. the fish had to spend energy to convert alpha-linoleic acid (ALA) to DHA] and consequently lower growth (Závorka *et al.*, 2021). Such energetic trade-offs may be exacerbated in extreme conditions, such as winter, where survival is contingent on successful accumulation and regulation of energy stores.

Other membrane lipids can provide important performance enhancement at suboptimal temperatures. Hassett & Crockett (2009) found that copepod growth was limited by dietary cholesterol content in both their cold (6 °C) and warm (25 °C) treatment temperatures. Hassett & Crockett (2009) sampled the cholesterol content of nine species of copepods across a range of habitat temperatures and found a positive correlation between the amount of cholesterol present and habitat temperature as well as the species' upper thermal tolerance.

While dietary lipid *quality* clearly impacts ectotherm thermal performance as discussed above, there is no consensus on how optimal dietary lipid *quantity* changes with temperature. Atlantic salmon consuming diets with a higher proportion of lipids and a lower proportion of indigestible materials (e.g. cellulose, rutin) exhibited higher growth rates, faster development times, and quicker maturation times regardless of the treatment temperature (Jonsson, Jonsson & Finstad, 2013). However, in a similar study on rohu (*Labeo rohita*), optimal lipid concentration changed with temperature (Mishra & Samantaray, 2004). Sealey *et al.* (2012) showed that juvenile sucker fish (*Chasmistes liorus*) fed high-lipid diets had higher growth rates than those fed low-lipid diets across temperatures and dietary protein content. However, the fish fed the highest protein and lipid diet had reduced thermal tolerance at the warmest treatment temperature. Other studies have found similar trends, where high lipid content does not necessarily confer better thermal performance (Guerreiro *et al.*, 2012).

Previous studies have revealed that at least some ectotherms are capable of preferentially selecting diets based on their lipid composition at different temperatures and that lipid composition can (but does not always) affect performance in ways predicted by homeoviscous adaptation. However, there are several gaps in our understanding of dietary lipid effects on ectotherm thermal biology. Most lipid research has focused on the effects of fatty acids on growth and thermal limits. These studies were most often performed on juvenile aquaculture fish using formulated diets that varied in dietary oil type (see Section IV.3). However, it is important to consider the diverse roles lipids play in cell biology. Fatty acids are the backbone of many different lipid classes that perform diverse cellular and organ-level functions. For example, phospholipids and sterols are key components of biological membranes, triacylgycerides are commonly used in energy storage, and certain long-chain polyunsaturated fatty acids can regulate metabolic gene expression by binding to various transcription factors (Hochachka & Somero, 2002; Turchini *et al.*, 2022). Lipids are also a primary energy source for most fishes, but digestive energetics differ across lipid classes (Turchini *et al.*, 2022). The more hydrophobic a lipid is, generally the more difficult it is to digest and assimilate, thus saturated or longer chain fatty acids are less digestible than polyunsaturated or short-chain fatty acids (Bogevik *et al.*, 2010; Bowyer, Qin & Stone, 2013). Lipids also vary in their energy density, with longer chain saturated fats providing greater energy per unit molecule than short chain or unsaturated fats. From our understanding of homeoviscous adaptation and the energetics of lipid biosynthesis and assimilation, it follows that ectotherms limited to diets containing suboptimal lipid quality and quantity at a given temperature may have a reduced capacity for membrane plasticity and impaired metabolism, which could scale to whole-animal performance.

It is also important to consider the timescale over which dietary lipids affect performance, especially for ectotherms living in variable environments. Homeoviscous adaptation occurs rapidly in some ectotherms (Williams & Hazel, 1994; Wodtke & Cossins, 1991). For example, Williams & Somero (1996) found that the intertidal mussel *Mytilus californianus* remodelled its phospholipid membranes during tidal cycles over a matter of hours and did so repeatedly. This acute response suggests that lipid remodelling may be an everyday coping mechanism used by ectotherms living in highly variable environments. If ectotherms do not have access to the pool of lipids needed to facilitate these responses, then rapid membrane plasticity may either not be possible, or require *de novo* synthesis using desaturases or elongases. It will be interesting to consider in future work whether ectotherms in highly variable environments prefer diets with high lipid content and diversity to enable rapid membrane plasticity changes.

Finally, lipid composition may affect metabolic signalling and stress at suboptimal temperatures. Reactive oxygen species (ROS) can damage cell membranes through a process called lipid peroxidation (LPO). High levels of LPO can cause cellular damage that leads to apoptosis. Fatty acids vary in their vulnerability to LPO, with polyunsaturated fatty acids being especially vulnerable (Hulbert, 2008). The overall susceptibility of a tissue to LPO, or the peroxidation index, is associated with a shortened lifespan in some species (Hulbert, 2008; Munro & Blier, 2012). Higher concentrations of protein and lipid in the diet are associated with higher ROS production, and ROS production often increases with temperature (Coggins *et al.*, 2017; Hwang & Lin, 2002). Importantly, dietary antioxidants like vitamin C and vitamin E can counteract ROS and reduce LPO, which may help mitigate the effects of extreme temperatures on cellular damage (see Section III.3).

(3) Other dietary nutrients, supplements and signalling molecules

Beyond broad macronutrients, numerous other dietary components (e.g. vitamins, minerals, specific nutrients, enzymes) which perform a wide variety of functions in the body (e.g. enzyme co-factors, signalling molecules, antioxidants) could potentially alter thermal performance in ectotherms. For example, some prey of lake trout (*Salvelinus namaycush*) contain high amounts of the enzyme thiaminase which can cause thiamine deficiency in their predators, thereby impairing their thermal performance (Baker *et al.*, 2023). Much of the research on these dietary components has been carried out to inform feeding regimes for farmed animals and has explored the effects of antioxidant content and amino acids or their derivatives on growth and tissue quality across temperatures.

Antioxidants (i.e. glutathione, vitamin C, vitamin E, spermine, etc.) scavenge ROS. As temperatures rise, ROS production generally increases (Coggins *et al.*, 2017; Hwang & Lin, 2002). Extreme acute or prolonged cold exposure can also induce oxidative stress (Lu *et al.*, 2019). Therefore, diets with higher antioxidant concentrations may benefit organisms that are under thermal stress by increasing their antioxidant capacity. This has been tested in a small number of studies. Coggins *et al.* (2017) examined the effect of supplementation of the antioxidant glutathione on thermal tolerance, antioxidant capacity, and LPO in *Daphnia magna* and found that as glutathione concentration increased, so did the antioxidant capacity of *D. magna*. However, glutathione supplementation did not alter *D. magna* LPO or thermal tolerance. Similarly, Ilham & Fotedar (2016) found that selenium supplementation (glutathione peroxidase, which is a vital antioxidant enzyme in red blood cells, contains Se) increased growth at lower temperatures and red blood cell count and glutathione peroxidase activity across temperatures in yellowtail kingfish (*Seriola lalandi*). Hwang & Lin (2002) tested the effects of vitamin C supplementation on thiobarbituric acid reactive substances (TBARS; a by-product of LPO) at 25 °C and 35 °C. The 35 °C treatment caused higher LPO, which was reduced by dietary addition of vitamin C. Finally, Lu *et al.* (2019) found that antioxidant supplementation in zebrafish (*Danio rerio*) diets increased the survival and liver catalase activity of the fish during a cold-shock experiment relative to control diets. By contrast, Olsen, Løvaas & Lie (1999) tested the interactive effects of the antioxidant spermine, dietary polyunsaturated fatty acid content, vitamin E concentration, and acclimation temperature (0.6 °C and 12 °C) on Arctic char (*Salvelinus alpinus*) and found no evidence that increasing vitamin E above baseline levels or supplementing the diet with spermine altered oxidative stress across temperatures (oxidative stress was measured using TBARS assay as an indicator of LPO). While there is evidence that antioxidant supplementation can increase antioxidant capacity, the impacts of this on performance, oxidative stress and thermal tolerance were less consistent across studies and may depend on whether the acclimation temperature fell within the optimal range for the species, as oxidative stress often increases under thermal stress.

Dietary concentrations of essential and non-essential amino acids (e.g. L-carnitine, L-tryptophan, β-alanine) can also alter thermal performance in ectotherms. For example, Akhtar *et al.* (2013) found that dietary supplementation with L-tryptophan mitigated the effects of heat and salinity stress in rohu. Lamb & Loschiavo (1981) observed an interactive effect of dietary lysine concentration and temperature on development rates in larval beetles (*Tribolium confusum*), with high lysine plus high temperature treatments conferring the fastest development times. Dixon *et al.* (2023) showed that brook char (*Salvelinus fontinalis*) fed a β-alanine-supplemented diet had lower cardiomyocyte uptake of the β-amino acid taurine, which led to a reduction in maximum heart rate across a thermal gradient and improved upper thermal tolerance. Dietary L-carnitine (important in lipid metabolism) supplementation in the cichlid fish *Pelvicachromis pulcher* increased survival rates during a cold-shock experiment (Harpaz, Becker & Blum, 1999), but had no effect on guppy (*Poecilia reticulata*) reproductive success across temperatures (Dzikowski *et al.*, 2001). While there are many amino acids and their derivatives that could influence thermal responses in ectotherms, it is resource and time intensive to investigate how the dietary concentration of each may impact thermal performance. However, for farmed animals, identifying the optimal concentration of these feed components could help to mitigate thermal stress and improve performance, ultimately saving money.

An area for future study is the relationship between dietary hormones and temperature. In ectotherms, endogenous hormone production and activity are temperature sensitive (Farrell, 2011), and exogenous hormones from food can be assimilated and may have interactive effects with environmental conditions. For example, thyroid hormone regulates thermal acclimation responses in zebrafish and cannot be synthesised *de novo* by some invertebrates, including some larval echinoderms (Little *et al.*, 2013; Little & Seebacher, 2014). Dietary thyroid hormone alters growth and body composition (i.e. lipid, water, protein, ash content) in red drum (Moon, MacKenzie & Gatlin, 1994) as well as development rate and metabolism in many marine invertebrates (Little & Seebacher, 2014). It is conceivable that thermal acclimation responses may be affected by dietary thyroid hormone concentration, especially in ectotherms that do not synthesise thyroid hormone *de novo*. Thyroid hormone is one of many hormones that could be assimilated from the diet and interact with temperature to alter performance in ectotherms.

Dietary microRNAs (miRNAs) could also potentially impact thermal performance in ectotherms, although there is little research exploring this possibility to date. miRNAs are small, non-coding RNAs that act by silencing genes and thus play a key role in many biological processes such as cell differentiation, apoptosis, immune function, reproduction, and the stress response (Raza *et al.*, 2022). In fish, miRNAs can be differentially expressed in response to cold and warm temperatures (Raza *et al.*, 2022) and have been suggested to potentially target regulatory enzymes for glucose and lipid metabolism (Blödorn *et al.*, 2021). Traditionally, miRNAs were considered to be synthesised and utilised endogenously; however, there is increasing evidence that miRNAs can be incorporated from exogenous sources to act as cross-kingdom gene regulators (Zempleni *et al.*, 2015; Zhang *et al.*, 2019). For example, the parasitic plant dodder (*Cuscuta campestris*) can transport miRNAs to its host plant to silence host genes and enhance its own growth (Shahid *et al.*, 2018). miRNAs from food can also be absorbed through the digestive system, into the circulatory system and delivered to tissues (Zhang *et al.*, 2019). However, evidence of dietary miRNAs playing a functional role is equivocal in humans and animals (Zhang *et al.*, 2019), and this remains an exciting avenue for future investigation.

(4) Digestive physiology

Ectotherm digestive systems are diverse and vary as a function of age, sex, diet strategy, species, taxon, environmental conditions, and body size (Andrade *et al.*, 2005; Starck, 2003). However, the multifunctional digestive system is ubiquitously important for nutrient uptake, osmoregulation, and immune function and represents a substantial proportion of ectothermic energy budgets (Andrade *et al.*, 2005; Grosell, Farrell & Brauner, 2010). For example, the gut in some fish is estimated to account for 25% of cardiac output in non-digesting individuals (Farrell, 2016). While the separate effects of diet and temperature on digestive physiology have been extensively studied in ectotherms, their combined effects remain poorly understood.

The metabolic cost of digestion, or specific dynamic action (SDA), is the increase in metabolism that occurs during the consumption, digestion, absorption, and assimilation of a meal (Secor, 2009). It is well documented that SDA is positively correlated with both the energetic content of a meal and meal size (Secor, 2009). However, other diet-specific impacts on SDA are uncertain due to differences in findings across studies. For example, protein digestion, assimilation, and synthesis are considered to comprise a large portion of the SDA response (for an extensive review see Secor, 2009; Andrade *et al.*, 2005); however, some studies report no differences in SDA in response to changes in dietary protein concentration [using isocaloric diets with varying protein to lipid ratios in rainbow trout (*Oncorhynchus mykiss*); Eliason, Higgs & Farrell, 2007]. Few studies have measured SDA for different meal types, across a temperature range (Pérez-Casanova, Lall & Gamperl, 2010; Stiller *et al.*, 2017). Pérez-Casanova *et al.* (2010) measured SDA in Atlantic cod (*Gadus morhua*) and haddock (*Melannogramus aeglefinus*) in response to different dietary protein to lipid ratio at 2 °C, 6 °C, and 11 °C. While diet did not affect the SDA response, temperature increased resting metabolism and total SDA. Notably, this research employed isoenergetic diets with relatively small differences in macronutrient content (11 *versus* 16% lipid), and measured SDA on fish fed to satiation (i.e. meal size was not standardised to body mass; Pérez-Casanova *et al.*, 2010).

While diet and temperature can separately affect the SDA response, it is difficult to resolve the mechanisms underlying those differences or predict their interactive effects. The digestion and assimilation efficiency of specific nutrients/macronutrients can change with temperature in complex ways. For instance, Plasman *et al.* (2019) measured the SDA response in lizards (*Agama atra*) held at 20 °C, 25 °C, or 32 °C. Consistent with known temperature effects, peak SDA increased and gut passage rates decreased at higher temperatures (although total SDA, i.e. the integral under the SDA curve, did not change). While total SDA remained the same, protein assimilation increased, and lipid and protein were oxidised on different timescales, with proteins metabolised first across temperatures (Plasman *et al.*, 2019). Clissold *et al.* (2013) found completely different patterns of macronutrient digestibility in locusts (*Locusta migratoria*) fed kangaroo grass (*Themeda triandra*) or wheat (*Triticum aestivum*) seedlings after acclimation to 32 °C or 38 °C. Carbohydrate absorption was higher at 32 °C, while protein absorption was higher at 38 °C, but only on the kangaroo grass diet. In wheat seedling-fed locusts, the ratio of carbohydrate to protein absorbed did not change with temperature.

For other measures of digestive physiology, investigations of interactions between diet and temperature effects have found mixed results. For example, Castañeda *et al.* (2006) did not find a difference in intestinal morphology or activity of digestive enzymes (e.g. aminopeptidase-N and maltase) between Chilean giant frog tadpoles (*Caudiverbera caudiverbera*) fed rat chow or spinach. However, temperature did alter digestive enzyme activity and higher temperatures were associated with shorter gut lengths compared to cold-treated tadpoles (Castañeda *et al.*, 2006). Similarly, inclusion of prebiotic fructo-oligosaccharides did not affect most digestive enzymes (e.g. lipase, α-amylase) or gut morphology in gilthead sea bream (*Sparus aurata*) held at 18 °C or 25 °C, with the exception of an interactive effect of diet and temperature on total alkaline protease activity in the posterior gut (Guerreiro *et al.*, 2016). By contrast, Mazumder *et al.* (2018) found that diet (pellet *versus* shrimp) and temperature had separate (but not interactive) effects on relative gut length and pepsin activity in Malabar blood snapper (*Lutjanus malabaricus*), where pepsin activity was higher on the shrimp diet and relative gut length was lower. These results demonstrate how complex the combined effects of diet and temperature can be on digestive physiology, especially when exploring the effects of very different diets.

Overall, there is an urgent need for more research on diet and temperature effects on digestive physiology in ectotherms. A few considerations are listed below. First, some animals can supplement consumption with nutrient absorption directly from the environment through their skin (Glover, Blewett & Wood, 2016), or gills (Blewett & Goss, 2017), which should be included within their energy budget across temperatures. Second, energetic investment in digestive tissue maintenance and function can vary with diet strategy and feeding frequency. For example, herbivores have longer guts than closely related omnivores, and carnivores (Caruso & Sheridan, 2011; Horn, 1989). Gut morphology and surface area are also highly plastic traits that can change in response to diet, temperature, and feeding frequency (Behrens & Lafferty, 2012; Mazumder *et al.*, 2018). In herbivores, the cost of digestive tissue maintenance may be higher than that of carnivores. For animals that feed less frequently, like snakes, or undergo seasonal changes in feeding frequency (e.g. overwintering and hibernating animals), the costs of digestion and digestive tissue maintenance may vary depending on the time since the last meal and season. These variations in diet strategy across taxa could interact with temperature in unique ways. Moving forward, we should pursue integrative studies that assess several measures of digestive physiology across levels of biological organisation (from cellular to metabolism to growth). This will help to clarify diet and temperature effects on digestion, assimilation, and SDA relative to an individual's overall energy budget.

Ectotherms may also modify their diet selection or ingestion rate to ensure that their overall energy budget is not constrained. As temperatures warm, standard metabolic rate (i.e. the energy required for basic maintenance functions such as protein turnover, respiration, etc.) typically increases exponentially while maximum metabolic rate (i.e. the peak metabolism possible) increases to a point and then usually plateaus or declines. The difference between maximum and standard metabolic rate is termed the aerobic scope and represents the aerobic capacity of an animal to perform fitness-enhancing tasks (e.g. locomotion, digestion, reproduction). During postprandial metabolism, oxygen uptake increases until peak SDA (which scales with meal size). Any remaining aerobic scope during digestion is termed the postprandial residual aerobic scope and represents the remaining capacity of animals to allocate oxygen to other activities (e.g. exercise, vigilance against predators, foraging, etc; Jutfelt *et al.*, 2021). At suboptimal temperatures, an animal's aerobic scope can decrease, while simultaneously, its energetic capacity to digest/assimilate a meal effectively and perform other fitness-enhancing activities becomes constrained. In this case, animals may consume smaller meals to conserve their energetic capacity for other fitness-enhancing functions (Eliason, Van Wert & Schwieterman, 2022; Jutfelt *et al.*, 2021, Norin & Clark, 2017). An alternative, but untested hypothesis is that animals exposed to thermal stress may alter their diet choices to less energetically expensive options to reduce their peak SDA and conserve their postprandial residual aerobic scope. It should be noted, though, that (*i*) at extreme temperatures, animals often cease feeding entirely and (*ii*) there are notable exceptions, like lionfish (*Pterois* sp.), which appear to be released from predation pressure and eat maximally even under thermal stress (e.g. Steell *et al.*, 2019).

(5) Microbiome

The microbiome has wide-ranging effects on host physiology, with studies demonstrating a role in host digestive performance, health, locomotory performance, cardiovascular function, growth, development, behaviour, and even thermal tolerance (Fontaine & Kohl, 2023; Fontaine, Mineo & Kohl, 2022; Henry & Colinet, 2018; Kohl & Carey, 2016; Moeller *et al.*, 2020; Semova *et al.*, 2012; Schretter *et al.*, 2018). Ectotherm intestinal microbiomes are fascinating communities because they must tolerate the same changes in environmental conditions as their host (e.g. temperature, salinity), while simultaneously coping with variation in nutrient availability (i.e. host diet), and habitat structure (i.e. intestinal morphology). There is clear evidence that temperature and diet can separately affect gut microbiome composition, but their combined effects remain poorly understood (Ayayee *et al.*, 2020; Bestion *et al.*, 2017; Fontaine, Novarro & Kohl, 2018; Piazzon *et al.*, 2017; Ramsby *et al.*, 2018).

Diet accounts for a significant proportion of observed variability in microbiome composition in wild animals (Clements *et al.*, 2014; Kohl & Carey, 2016; Piazzon *et al.*, 2017). Microbes can alter host physiology through nutrient provisioning and metabolite signalling (i.e. short-chain fatty acids, amino acid derivatives, vitamins, etc.), and the activity of the microbiome and production of these molecules depends on host nutrition (Kohl & Carey, 2016). For example, Ayayee *et al.* (2020) found that diet altered the provisioning of essential amino acids by the gut microbiome in the cockroach *Diploptera punctata*, which may have contributed to observed changes in the animal's standard metabolic rate.

Temperature has considerable impacts on microbial physiology and microbiome community composition and thus, host physiology [Trevelline *et al.*, 2019; in amphibians (Fontaine *et al.*, 2018), reptiles (Bestion *et al.*, 2017; Moeller *et al.*, 2020) and sponges (Ramsby *et al.*, 2018)]. Warming has been associated with reductions in microbiome species diversity for some ectotherms. For instance, lizards (*Zootoca vivipara*) held under a climate change scenario (2–3 °C elevated) temperature treatment had a 34% reduction in gut microbiome species diversity compared to those held under ambient conditions (26.6 °C average; Bestion *et al.*, 2017). Notably, survival rates among the lizards over a year later were positively correlated with microbiome species diversity. Fontaine *et al.* (2018) found similar effects of suboptimal temperatures reducing microbial diversity in the gut microbiome of salamanders (*Plethodon cinereus*). Further, changes in microbiome composition of wild-caught western fence lizard (*Sceloporus occidentalis*) during experimental warming were related to the lizard's heat tolerance (Moeller *et al.*, 2020). For organisms like corals, whose health is reliant on microbial symbionts, temperature alters coral health directly through coral bleaching, where the coral expels its symbiotic partners in response to elevated temperatures. Interestingly, Rosado *et al.* (2019) found that corals (*Pocillopora damicornis*) inoculated with beneficial microbes had lower levels of bleaching at high temperatures and reduced bleaching in response to pathogen challenge. Similarly, aphids (*Acyrthosiphon pisum*), had thermal limits that were determined by the lethal temperature of their symbiotic bacterium (*Buchnera aphidicola*; Dunbar *et al.*, 2007).

If sub-optimal temperatures negatively affect microbiome composition and function and anthropogenic stress causes changes in food availability and quality, then the interaction of these two environmental stressors could be detrimental to animal health. We identified only three studies that explored the simultaneous effects of diet and temperature on microbiome composition. One study independently assessed diet and temperature effects on abalone (*Haliotis discus hannai* and *H. discus hannai* × *H. fulgens hybrids*) microbiomes (i.e. non-factorial design; Wang *et al.*, 2020). The core microbiome in their study remained stable, but there were some differences in microbiome composition in response to diet and temperature. Guerreiro *et al.* (2016) found no effect of dietary inclusion of prebiotic fructo-oligosaccharides on microbiome composition in gilthead sea bream held at 18 °C or 25 °C. In the third study, dietary lipid composition and temperature interactively influenced microbiome composition in yellowtail kingfish: the diet with the highest lipid content rescued the effects that the lower temperature treatment (20 °C compared to 26 °C) had on microbial diversity (Soriano *et al.*, 2018). It should be noted that the results of this study demonstrated a stronger effect of temperature than diet, but the authors argue that this was because their diet treatments were quite similar. Given the growing body of evidence demonstrating separate effects of diet and temperature on host–microbe interactions, it is essential that researchers continue to investigate how microbiomes are affected by a multi-stress environment, how these changes alter host physiology, and whether it is possible to mitigate these effects.

Understanding the functional consequences of microbiome community changes is technically challenging, especially in wild animals. As a result, the study of host–microbe interactions on ectotherm environmental physiology has primarily focused on invertebrate species and species that have a symbiotic microbial partner (Fontaine & Kohl, 2023). In many cases, much of the evidence linking microbiome composition and host thermal physiology is correlative. However, researchers have been able to directly test how changes in the microbiome impact wild animal physiology using combinations of metabolomics, microbiome manipulations, gnotobiotic animals, RNA sequencing, proteomics, metagenomics, imaging, microbial culturing, and other techniques. For example, recent studies using microbiome manipulations offer evidence of the importance of the gut microbiome in ectotherm plasticity and how diet and temperature mediate these changes (Fontaine *et al.*, 2022; Trevelline & Kohl, 2022). In one study, microbiome disruption lowered critical thermal maxima and raised thermal minima in wild green frog tadpoles (*Lithobates clamitans*) (Fontaine *et al*., 2022). Trevelline & Kohl (2022) found that gut microbiome composition altered diet selection in mice (*Mus musculus*). These results highlight how the microbiome is a central player in ectotherm ecological physiology.

(6) Quantity *versus* quality

Similar to changes in food quality, food restriction (and energy density) can alter an ectotherm's energy balance and nutrient assimilation, which can have downstream impacts on its thermal limits (e.g. $\mathrm{CT_{max}}$, temperature that induces cardiac arrhythmia), behaviour (e.g. foraging time, behavioural thermoregulation), and TPCs for growth, metabolism, cardiac performance, and others. While not always the case (Lee *et al*., 2016; Mclean & Todgham, 2015; Rodgers *et al*., 2019), food restriction can reduce ectotherm thermal breadth (e.g. Lee *et al*., 2016; Nyamukondiwa & Terblanche, 2009; Woiwode & Aidelman, 1992). Some animals may behaviourally thermoregulate to compensate for food restriction by moving into cooler areas that lower their metabolic demands; a response termed 'behavioural hypothermia' (Rodgers *et al*., 2019; Gilbert & Miles, 2016; reviewed in McCue, 2010) or to optimise their foraging and digestive energetics (Brewitt, Danner & Moore, 2017). Predator–prey interactions can also be affected by food restriction and temperature, as demonstrated in Lienart *et al*. (2014), where juvenile damselfish did not respond to predator cues when exposed to simultaneous heat and food stress but showed risk-averse responses when food was abundant or in cooler water. This indicated that when conditions were stressful, the fish were more likely to put themselves at risk to meet their energy needs. These types of behavioural shifts are important to consider because they influence how animals navigate their environment and interact with one another, which ultimately, affects their ecosystem functions.

In addition to thermal limit and behavioural changes, growth typically decreases with food restriction, and the optimal temperature for growth and thermal breadth is also expected to decrease when animals eat less (Brett,

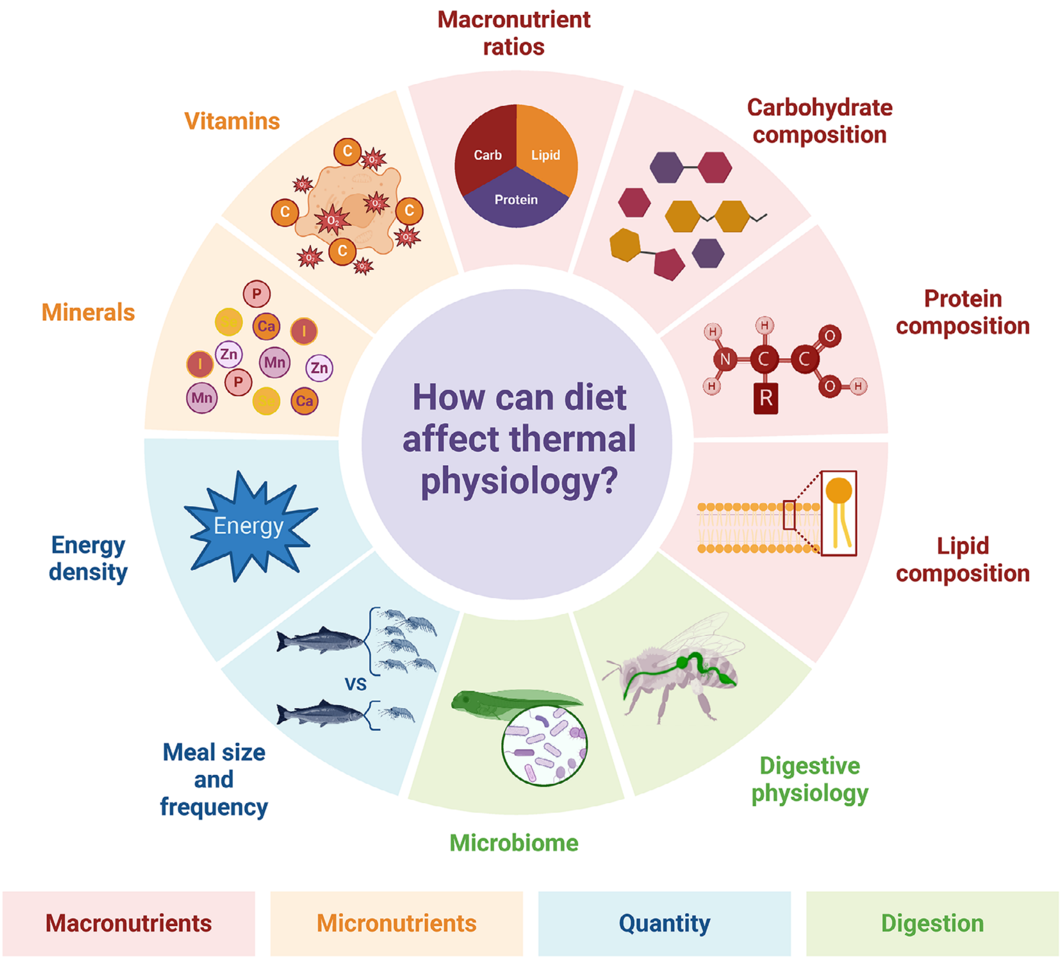

Fig. 4. Aspects of diet and digestive physiology that may interact with temperature to influence ectotherm physiology and ecology. There are many potential interactions, those that have been studied in most detail are discussed in Section III. Created with biorender.com.

Shelbourn & Shoop, 1969; Brett, 1971; Huey & Kingsolver, 2019). These observations suggest that the range of temperatures an ectotherm can truly thrive in may be limited by resource availability. When considering how to manage species and populations of interest under climate warming, individuals living in resource-poor, less biodiverse, and degraded habitats may be at greater risk of extirpation than those living in pristine environments, even if the populations have the same performance when brought into the laboratory and held under common conditions. In these cases, higher quality foods may rescue some of the negative impacts of food restriction on behaviour and thermal limits. Thus, it is critical that food availability and quality for ectotherms in the wild are considered in experimental design and conservation management (Fig. 4).

IV. ECOLOGICAL AND ENVIRONMENTAL CONSEQUENCES OF CHANGING DIET WITH TEMPERATURE

The interactions between the amount of food animals consume, the quality of that food, and environmental temperature can have significant impacts on ectotherm physiology, behaviour, environmental tolerance, and ultimately, ecology. The extent to which these factors influence performance depends on how much ingestion is reduced, the exact nutritional differences in the diet(s), the animal's prior nutritional state, and the surrounding environmental conditions. In this section, we discuss some of the broader ecological impacts of these factors.

(1) Species distributions and range shifts

As temperature profiles and environmental landscapes shift, previously occupied habitats may become unsuitable, while others may become more favourable (Deutsch *et al.*, 2008; Pinsky, Comte & Sax, 2022). Species distributions have been evaluated through ecological and thermal biology lenses, which has offered insight into ectotherm biogeography (Deutsch *et al.*, 2008, 2015; Fredston *et al.*, 2021; Pinsky *et al.*, 2019, 2022; Sunday, Bates & Dulvy, 2011; Sunday *et al.*, 2014, 2019). Physiological thermal tolerance and species interactions (e.g. competition, predator–prey interactions) are both important for determining species range limits. Diet interacts with both axes – it can alter thermal performance and is dependent upon the species that can co-exist under those conditions. Thus, diet strategy and nutrition may also be critical factors determining a species' success and range movements.

For example, consider the distribution of herbivorous and omnivorous fishes in the Northern Hemisphere, which is characterised by high biodiversity (as measured by species richness) at the equator, but diminishes as latitude increases and water temperature decreases (González-Bergonzoni *et al.*, 2012; Floeter *et al.*, 2005; Vejříková *et al.*, 2016; for critique, see Clements, Raubenheimer & Choat, 2009). One leading explanation for this phenomenon is that cold water limits herbivorous fish digestion efficiency (through limitations on their microbiome function) to the point where they are unable to meet their metabolic demands on a plant-based diet: this is the temperature physiological constraint hypothesis (TPCH). The TPCH suggests that as water warms, the ranges of herbivorous fishes may shift towards higher latitudes (i.e. following warmer water) and omnivorous fish may consume greater proportions of algae in their diets, which could dramatically alter subtropical and temperate ecosystems (Behrens & Lafferty, 2007, 2012; Floeter *et al.*, 2005; González-Bergonzoni *et al.*, 2012; Vejříková *et al.*, 2016).

This hypothesis has been debated, with critics arguing that fish in the Southern Hemisphere do not follow the same distribution pattern as those in the Northern Hemisphere, (Clements *et al.*, 2009). For example, diet choice and species distribution trends were not consistent with this hypothesis in the wild for the common herbivorous fish rarī (*Odax pullus*) (Johnson *et al.*, 2020; Trip *et al.*, 2014). Additionally, a recent meta-analysis did not find support for the TPCH governing herbivorous fish digestion across temperatures (Knight, Guichard & Altieri, 2021). These studies discuss alternative hypotheses, such as evolutionary constraints, that could also explain the observed distribution patterns. Clearly, examining these mechanistic links is challenging and requires input from nutritional ecologists, evolutionary biologists, and comparative physiologists. While an active area of research, this example highlights how species distributions may be limited in some ways by their nutritional resources, digestive physiology, or environmental conditions.

(2) Behavioural thermoregulation

When faced with unfavourable temperatures, ectotherms can acclimate (within-generation), use transgenerational plasticity (between generations), adapt (over many generations), or move to a more suitable habitat (Hofmann & Todgham, 2010). Moving requires a heterogenous environment where preferred temperature(s) are accessible to the animal. For example, some salmonids move between warmer prey-dense water to forage and cooler thermal refuges to optimise energetics (Brewitt *et al.*, 2017). There is evidence from laboratory experiments that ectotherm temperature preference changes when fed different dietary lipid treatments (Brzeziński & von Elert, 2015; Geiser *et al.*, 1992). For example, Brzeziński & von Elert (2015) demonstrated that certain *Daphnia* sp. only perform diel migrations from warm water (associated with higher predator abundance) to cold water (associated with fewer predators) when fed a diet supplemented with EPA, but not in response to cholesterol supplementation. Similarly, bobtail lizards (*Tiliqua rugosa*), lowered their selected body temperature by 3–5 °C after being fed a diet high in unsaturated fats compared to lizards fed a diet high in saturated fats (Geiser *et al.*, 1992). Differences in lipid quality seem to affect behavioural thermoregulation in ways predicted by homeoviscous adaptation.

Other animals change their selected body temperature when fed diets that differ in macronutrient composition, presumably to optimise their energetics. For example, Coggan, Clissold and Simpson (2011) held locusts (*L. migratoria*) at 32 °C and fed them diets consisting of the same protein to carbohydrate ratio, but that differed in the total amount of protein and carbohydrate in the diet (between 15 and 42%) to vary the diet's energy density. As nutritional quality (i.e. higher gross amount of protein and carbohydrates, with more energy available) increased, locusts preferred warmer temperatures that facilitated higher growth rates. By contrast, under nutrient-limited conditions, the locusts chose cooler temperatures that conferred high assimilation efficiency but lower growth. In another study, locusts fed kangaroo grass had higher protein absorption in warm conditions but higher carbohydrate absorption at cold temperatures (Clissold *et al.*, 2013). However, when the locusts were fed a different diet of wheat seedlings, their protein and carbohydrate absorption did not change with temperature. When subsequently deprived of carbohydrates for a few days, locusts preferred colder temperatures (maximised carbohydrate absorption), but only after being fed kangaroo grass (Clissold *et al.*, 2013). Locusts fed wheat seedlings preferentially chose warmer temperatures, irrespective of prior nutritional state, which maximised their growth. Thus, locusts were able to alter temperature preference based on prior nutritional history to maximise performance on diets that varied in their digestibility (Clissold *et al.*, 2013).

Most of the diet studies that measured behavioural thermoregulation focused on terrestrial species. In heterogenous environments where the capacity for thermoregulation can be higher, selecting the best temperature to maximise digestive energetics and growth may be more important than finding a diet that maximises performance at a given temperature. In other words, there may be a greater incentive for generalist diet strategies in heterogenous thermal environments, although this idea has yet to be tested. Lipid quality, in particular, seems to mediate several ecologically important behaviours and species interactions, such as predator avoidance (Brzeziński & von Elert, 2015) and behavioural thermoregulation (Geiser *et al.*, 1992) in ways that are consistent with homeoviscous adaptation. By contrast, ectotherms fed different macronutrient ratios appear to select body temperatures that optimise their energetics, with cooler preferred temperatures reducing growth but slowing metabolism and digestion and increasing or not affecting assimilation efficiency (Clissold *et al.*, 2013; Coggan *et al.*, 2011).

(3) Aquaculture

A substantial portion of the literature investigating interactions between diet and temperature is focused on aquaculture of fish and invertebrates, as there is an incentive to identify the best aquafeed ingredients to maintain optimal feed conversion ratios, health, and growth in a changing climate. Aquaculture is an important and growing food sector, but one with a variety of sustainability and logistical challenges. For fishes, these challenges include, but are not limited to, disease, parasites, interbreeding with native fish, introductions as invasive species, depletion of forage fish for fishmeal and fish oil, and pollution (Froehlich *et al.*, 2022; Jobling, 2016; Lafferty *et al.*, 2015; Stentiford *et al.*, 2017). Each of these issues may be exacerbated by suboptimal nutrition and temperature.

One of the challenges to aquaculture of fed fish (i.e. animals requiring commercial aquafeeds as opposed to filter-feeding animals or invertebrate grazers) is creating sustainable aquafeeds (Bowyer *et al.*, 2013). Forage fish have been commonly harvested for fish meal and oil production, which is unsustainable as a primary protein source given the rising demand for farmed fish (Oyinlola *et al.*, 2021). Farmers are interested in finding alternative protein and fat sources to supplement forage fish. Over time, aquaculture feeds have shifted to include proportionally more terrestrial ingredients (e.g. soybean, wheat, nuts, etc.) which has effectively lowered the trophic level of farmed seafood relative to their wild counterparts over the last 20 years (Cottrell *et al.*, 2021). Plant-meal is generally lower in protein and lacking the complete amino acid profile required for carnivorous fish; thus, these feeds require additional nutritional supplementation (Bowyer *et al.*, 2013; Cottrell *et al.*, 2021). Any differences in nutrition between farmed and wild fish may influence their plasticity and environmental tolerance. As discussed above, an ectotherm's optimal dietary macronutrient ratios may change with temperature, their dietary lipid composition can influence their thermal limits, and specific dietary amino acids and micronutrients may impact their thermal performance (see Section III).

When considering the costs and benefits of alternative protein and fat sources in aquaculture, these interactions require close examination. For example, lipid composition generally differs between terrestrial plant and fish oil, with fish oil being higher in certain omega-3 fatty acids (e.g. EPA and DHA). Further, some plants contain defensive secondary metabolites or anti-nutrient factors (e.g. tannins, lectins), some of which can be inactivated during feed preparation or upon heating. These will not be discussed in detail here, but for a comprehensive discussion of nutrition in aquaculture feeds, we recommend Jobling (2016) and Hardy & Kaushik (2021). 'Microbiome engineering' and prebiotic feed additives may be able to enhance digestion efficiency of plant protein and lipid sources or improve their immune response, antioxidant capacity, and thermal tolerance at suboptimal temperatures (for review, see Naiel *et al.*, 2022). Farmers may also be able to adjust feed across seasons to maximise thermal performance in farmed fishes and invertebrates. Exploring these interactions will be no small task given the time and resources needed for feeding and growth studies on farmed animals. Additionally, reliance on terrestrial crops incurs environmental costs that should be weighed against alternative ingredients (Cottrell *et al.*, 2021), although the environmental impacts of feeding farmed seafood is estimated to be lower than for their terrestrial counterparts (Froehlich *et al.*, 2018). While further investigation is required, ultimately such work could help advance sustainable aquaculture practices in a changing climate.

V. CONCLUSIONS

(1) Diet quality (i.e. macronutrient and micronutrient composition) can affect ectotherm thermal limits and the thermal sensitivity of several ecologically important traits, including metabolism, growth, digestion, and cardiac function.
(2) When an ectotherm's food availability, food options or dietary nutritional quality change, the animal may respond behaviourally by adjusting their diet or temperature selection. Temperature can also directly impact an ectotherm's nutritional needs, which the animal may compensate for by altering its consumption rate, foraging behaviour, and ultimately, its ecological role. In particular, macronutrient ratios and lipid composition can influence both diet preference and thermal preference in ectotherms.
(3) There are several notable gaps in our knowledge of how diet and temperature interact to affect ectotherm physiology. In particular, the microbiome is emerging as a critical player in thermal biology, digestive physiology, and diet selection. However, the combined effects of diet and temperature on microbiome function, and digestive energetics are understudied.
(4) The effects of diet and temperature change have far-reaching implications for ectotherm biogeography, ecology, and farming. We strongly encourage future work examining diet effects on ectotherm thermal performance. By understanding when and why diet and temperature interact, we can make more accurate and far-reaching predictions across taxa. More broadly, diet may help or hinder animals' ability to tolerate other anthropogenic stressors (e.g. salinity, desiccation, pH, hypoxia, pollution, etc.). This type of research requires diet and nutritional information for wild animals, which is notoriously difficult to obtain. Thus, this effort calls for close collaboration between physiologists and ecologists to identify species and environments of interest and to uncover the mechanisms driving the observed ecological trends.

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VII. REFERENCES

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. References and metadata for literature values shown in Fig. 3.

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