

Forum

How sharp is the knife? Herbivore and carnivore sensitivity to resource stoichiometric quality

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While understanding feeding preferences of herbivores and carnivores is of major importance in ecology, we still know very little on the sensitivity of different functional groups to suboptimal stoichiometric resource quality. Here, we apply concepts of ecological stoichiometry to shed light on differences in the nutritional requirements of herbivores and carnivores, and to make predictions on the influence of suboptimal resource stoichiometric quality on the fitness of these different consumers. Herbivores generally experience more variation in the quality of their resource than carnivores do, and these differences have likely shaped the extent to which coping mechanisms have evolved. Consequently, we expect 1) herbivores to maintain their stoichiometric homeostasis over a broader range of resource stoichiometry than carnivores, 2) the threshold elemental ratio (TER), i.e. the dietary carbon to nutrient ratio which maximizes fitness, of herbivores to be higher than that of carnivores, 3) a narrower and sharper knife-edge response in carnivores than herbivores and 4) asymmetric knife-edge responses indicating a higher sensitivity to the diet quality that consumers are not used to dealing with, namely nutrient limitation in carnivores and nutrient excess in herbivores. Our study poses that documenting the ranges of resource quality where consumer fitness declines in diverse organisms is a very promising avenue to increase our understanding of community composition and food web functioning.

Keywords: ecological stoichiometry, food web, knife-edge hypothesis, stoichiometric homeostasis, threshold elemental ratio, trophic mode

Introduction

To function and grow, life requires energy, as well as elements and nutrients which are incorporated and combined into cellular components. Organisms have evolved a large variety of strategies to obtain these substances, and many have specialized in feeding on



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specific resources. For instance, heterotrophic organisms can obtain organic matter by feeding on autotrophs (herbivory) or on other heterotrophs (carnivory). Logically, obtaining resources in sufficient amounts is crucial, but besides the obvious importance of the quantity of resource available, resource quality also drives the dynamics of consumers by affecting their fitness (Sterner and Elser 2002, White 2005, Arts et al. 2009).

While biochemical contents, for example lipids or proteins, have been used to characterize resource quality (White 2005, Arts et al. 2009, Simpson and Raubenheimer 2012), the recognition of the importance of elemental stoichiometric constraints between consumer needs and resource nutrient content has increased our understanding of trophic interactions further (Sterner and Elser 2002). Through the study of the balance of energy (carbon, C) and multiple chemical elements (e.g. nitrogen, N, and phosphorus, P, but also other ones, Jeyasingh and Pulkkinen 2019) in ecological interactions, the framework of ecological stoichiometry has identified that the elemental composition of organisms may vary to different degrees depending on the taxon or trophic level considered. These differences can be linked to specific degrees of stoichiometric homeostasis (Persson et al. 2010, Meunier et al. 2014), that is, the ability of organisms to keep the chemical composition of their body constant, despite changes in the chemical composition of their resources (Kooijman 1995). Because autotrophs are typically non-homeostatic, their carbon to nutrient stoichiometry (e.g. C:N and C:P ratios) varies widely, whereas heterotrophs tend to keep their elemental ratios within a much narrower range (Sterner and Elser 2002, Persson et al. 2010). The absence of stoichiometric homeostasis in autotrophs likely comes from the fact that these organisms obtain energy (mostly sunlight) and material from different, uncoupled, sources within their environment. Consequently, autotrophs developed strategies to store these resources, as the availability of one resource does not guarantee that of another one. When nutrient availability or light conditions change, acquisition and storage create the potential for large variations in the C:N:P ratios of autotrophs, which can be defined as conformers (Meunier et al. 2014). Conversely, stoichiometric homeostasis in heterotrophs has been associated with limited nutrient storage capacity; however, there is still considerable debate whether stoichiometric homeostasis is an advantageous strategy or a constraint (for synthesis Meunier et al. 2014). Elemental homeostasis is regulated via excretion, egestion, respiration, and ingestion. Interestingly, not all heterotrophs possess the same degree of stoichiometric homeostasis. Rather, they are distributed along a continuum from weakly homeostatic to strict homeostatic regulators. As the relative carbon to nutrient ratios in most consumers are less variable, and lower, as compared with that in autotrophs (Van de Waal et al. 2010), the potential nutritional imbalance that exists between consumers and their resource is generally larger for herbivores than for carnivores (Sterner and Elser 2002).

Given the ecological consequences of nutritional imbalances and limitations for population and community dynamics of heterotrophs, it is no surprise that identifying the conditions under which animal consumers experience

nutritional deficiencies in their food resources has been, and still remains, a major research topic in ecology (Sterner and Elser 2002, White 2005, Arts et al. 2009). A well-developed tool to assess the potential for nutrient limitation in heterotrophs is to determine their threshold elemental ratio (TER). The TER is the dietary nutritional composition which maximizes fitness, and thus represents optimal resource carbon to nutrient ratios (Frost et al. 2006). The TER is typically used for C:N and C:P ratios, but the optimal ratio between carbon (energy) and other nutrients obviously also exists for other elements (Chen et al. 2014), hence our use of C:X in the following text. Originally, the TER was defined as the point at which growth limitation of consumers switches from nutrient (e.g. N or P) to carbon limitation (Sterner and Hessen 1994, Sterner 1997). However, Boersma and Elser (2006) later on identified that an excessive nutrient supply can reduce growth. They introduced the knife-edge hypothesis which posits that the growth of consumers decreases above the TER because of nutrient limitation, and decreases below the TER because of nutrient excess. While this stoichiometric knife-edge prediction has been supported for a wide range of taxa (Elser et al. 2006b, Benstead et al. 2014, Bullejos et al. 2014b, Laspoumaderes et al. 2015, Elser et al. 2016, Zhou and Declerck 2019), to date, no synthesis has been made for different trophic levels. Indeed, the relative sensitivity of herbivores and carnivores to high and low C:X resources has been poorly described (Anderson et al. 2020), and no theoretical approaches have tackled this. Variations in the stoichiometric knife-edge between taxa are not anodyne as they reflect the i suboptimal resource quality, and may therefore be crucial for the understanding of a range of ecological patterns and processes, such as bottom-up control, trophic energy transfer efficiency and trophic cascade strength (Frost et al. 2006, Elser et al. 2016). We suggest that characterizing the idiosyncrasies of the response to nutritional mismatches may be very important to understand the sharpness of the knife edge response and any asymmetries around the TER for consumers, because these may have determined the extent of coping mechanisms adopted by consumers.

Here, we propose that linking the TER and stoichiometric homeostasis concepts can shed light on differences in the nutritional requirements of herbivores versus carnivores and allow us to make predictions on the fitness sensitivity (i.e. influence on growth, survival, and reproduction) of these different types of consumers to shifts in resource quality. These concepts address different aspects of growth and body composition responses to resource quality, and are therefore highly complementary. Herbivores often feed on resources of highly variable quality which often do not match their metabolic requirements, and, as a result, they have developed strategies to cope with suboptimal food supply (Pennings et al. 1993, White 2005, Behmer 2009, Hillebrand et al. 2009, Meunier et al. 2012, Herstoff et al. 2019). Importantly, nutritional mismatches are not constrained to plant–herbivore interactions. Homeostasis at the herbivore level reduces the scope for stoichiometric mismatch at the carnivore level, and the differences in the degree of stoichiometric

mismatches that are typically experienced by herbivores and carnivores may also have determined the extent to which coping mechanisms have evolved in these two types of consumers. This topic is particularly timely because human activities have altered, and will continue to alter, biogeochemical cycles and, in turn, the nutritional value of the resources consumed by herbivores and carnivores (Peñuelas et al. 2012, 2013, Sardans et al. 2012). Consequently, different sensitivities of herbivores and carnivores to suboptimal resource quality may create scope for important structural shifts in food webs.

Here, we explore the hypothesis that, due to the above-mentioned adaptations, herbivores are less sensitive in terms of growth response to resource quality alterations than carnivores, as the latter usually consume resources of high and stable quality. We expect 1) herbivores to maintain their stoichiometric homeostasis over a broader range of resource stoichiometry than carnivores. Given that herbivores generally consume resources with high C:X ratios whereas carnivores consume prey with low C:X ratios; we expect 2) the TER of herbivores to be higher than that of carnivores; and 3) a narrower and sharper knife-edge response in carnivores than herbivores. While the costs of nutrient excess for consumer growth are undeniable, the general consensus in the literature is that herbivores most often consume resources with C:X ratios above their TER. Those situations in which resources have excessively low C:X ratios are limited in time, as at the onset of a phytoplankton bloom, or are specific to geographic areas subjected to severe eutrophication, or linked to highly specialized high C:X herbivores such as aphids or humming birds (Sternler and Elser 2002, White 2005, Boersma and Elser 2006, Raubenheimer et al. 2009). Consequently, since herbivores are likely more often faced with resource C:X ratios above their TER and carnivores with C:X ratios below or close to their TER, we expect 4) asymmetric knife-edge responses indicating a higher sensitivity to the diet quality that consumers are not used to dealing with, namely nutrient limitation in carnivores and nutrient excess in herbivores.

Expectation 1: the homeostatic strength of herbivores is stronger than of carnivores

Because herbivores are more stoichiometrically homeostatic than plants, variations in the elemental content of autotrophs are buffered at the second trophic level by the stoichiometric homeostasis of primary consumers. As a result, carnivores generally do not experience as much variation in the quality of their resource as herbivores do. Under the assumption that homeostasis is an adaptive coping strategy, we hypothesize that differences in exposure to stoichiometric mismatch have likely shaped the extent to which coping mechanisms have evolved in herbivores and carnivores. More specifically, we expect carnivores to have lower physiological capacity than herbivores to maintain homeostasis in the face of stoichiometric mismatch (Fig. 1). Nutritional imbalances are transferred to carnivores when herbivore elemental composition varies due to strong stoichiometric mismatches

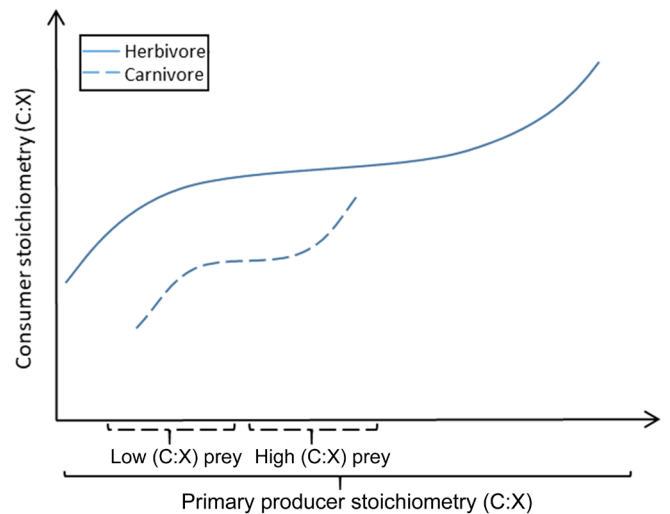


Figure 1. Generalized homeostasis patterns relating consumer stoichiometry to resource stoichiometry. The range of primary producer stoichiometries consumed by herbivores is broader than that of prey consumed by carnivores. Herbivores maintain their body stoichiometry stable over a broader range of resource stoichiometries than carnivores do, that is, herbivores have a stronger homeostatic strength than carnivores.

at the producer–herbivore interface (e.g. through herbivore plasticity or through compositional shifts in the herbivore community) (Boersma et al. 2008, Laspoumaderes et al. 2015). The limited evidence available from such situations indeed suggests that herbivores have a higher strength of homeostatic regulation than carnivores (Laspoumaderes et al. 2010, Meunier et al. 2014). While fewer data are available for carnivores than for herbivores, the current body of literature indicates that stoichiometrically imbalanced diets reduce the fitness of a wide range of predators (Jensen et al. 2012, Machovsky-Capuska and Raubenheimer 2020). Besides their influence on consumer fitness, prey of suboptimal quality have been shown to substantially alter the elemental composition of carnivores which can act as conformers even within a small range of food qualities (Schoo et al. 2014, Laspoumaderes et al. 2015), hence supporting our hypothesis that carnivores have a weak homeostatic strength.

Expectation 2: herbivores have higher TER than carnivores

Herbivores typically feed on resources with higher C:X ratios than carnivores (Sternler and Elser 2002, Van de Waal et al. 2010). We therefore hypothesize that herbivores have a higher TER than carnivores (Fig. 2) because they have evolved mechanisms that allow them to better cope with high C:X ratios (e.g. more efficient ways of eliminating excess C, higher assimilation efficiency of nutrients, lower excretion rates of nutrients) (White 2005). Interestingly, a study which used a stoichiometric model coupling animal bioenergetics and body elemental composition to estimate the TER of a

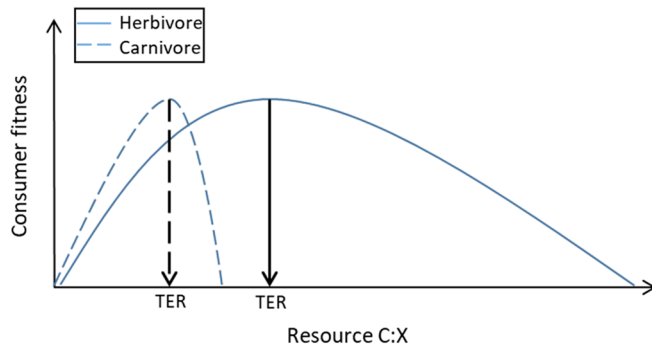


Figure 2. Generalized consumer fitness to resource stoichiometry response curves. Herbivores generally consume a broader range of resource stoichiometries and have a higher Threshold elemental ratio (TER) than carnivores. Because herbivores generally consume high C:X resources and carnivores generally consume low C:X prey, herbivores are likely more sensitive to low than to high resource C:X ratios whereas carnivores could be more sensitive to high than to low resource C:X ratios. These sensitivities are illustrated by asymmetric response curves.

broad range of aquatic consumers identified that the TER of carnivores is indeed particularly low (Frost et al. 2006), which supports our hypothesis. It is important to note that evolutionary drivers determining the TER may be not only linked to feeding conditions, but also to metabolic demands for growth rate (in the case of P) and other traits related to fitness (such as Ca). Despite the TER being a useful tool to assess the risk for nutrient limitation and the sensitivity to nutrient excess in heterotrophs, the number of studies which evaluate the fitness response of consumers to a broad range of resource C:X ratios is still too limited to allow a robust comparative analysis (Laspoumaderes et al. 2022).

Expectation 3: carnivores have a sharper knife edge than herbivores

In addition to being exposed to higher C:X food, herbivores are also typically confronted with higher variation in their food C:X than carnivores (Sternler and Elser 2002). Indeed, herbivores can be confronted with particularly low or high C:X food (Van de Waal et al. 2010), depending on the relative nutrient supply rates to their plant prey (e.g. eutrophic versus oligotrophic conditions). In contrast, variations in the C:X experienced by carnivores are strongly reduced due to the homeostatic capacity of their prey (Persson et al. 2010, Meunier et al. 2014). The evolved behavioural and physiological mechanisms that enable herbivores to consume a broad range of resource qualities are likely to lower the growth performance sensitivity of herbivores to variation in the elemental composition of the primary producers they feed on, resulting in a knife edge less sharp than that of carnivores (Fig. 2). In a study on shifts in organism's sensitivity to food quality constraints during ontogeny, Bullejos et al. (2014a) were the first to explicitly acknowledge that consumers may differ in the 'sharpness' of their knife edge (i.e. the rate at

which fitness decreases as resource stoichiometry deviates from the TER). Here, we expand on this idea and we suggest that the sharpness of the knife edge may not only vary within one species during ontogeny, but also between trophic levels. In support of this hypothesis, multiple studies have identified severe deleterious effects of diets imbalanced in macronutrients on the fitness of vertebrate and invertebrate predators (reviewed by Kohl et al. 2015). Using a narrow range of prey C:P ratios, Laspoumaderes et al. (2015) reported relatively low TER and sharp C:P stoichiometric knife edge at low prey C:P ratios in predatory copepods compared to herbivores, hence demonstrating that the stoichiometric knife edge does not only apply to herbivores but also to higher trophic levels which can be highly vulnerable to stoichiometric imbalances. Moreover, it is important to consider that the shape of the knife edge may be influenced by resource quantity, even within the same species (Hessen 1990, Urabe and Watanabe 1992). To test the idea that knife edge sharpness is stronger in carnivores than herbivores, experimental studies should be conducted to compare the growth responses to stoichiometric imbalance for representative samples of herbivores and carnivores, and these experiments should be conducted over appropriate gradients of resource C:X ratios.

Expectation 4: knife edge responses are asymmetric

Organisms may differ in their relative vulnerability to nutrient limitation versus nutrient excess. When confronted with high resource C:X ratios, consumers have to eliminate excess C and at the same time cope with limitation of X, whereas when exposed to low C:X they may have to cope with toxicity of X or costs related to its excretion (Zhou and Declerck 2019). These different challenges may result in different effects on fitness, implying that there may not be one, but two slopes determining the kurtosis of the curve on each side of the TER, essentially creating curves of different skewness. In order to test this hypothesis, we analysed the slopes on each side of the TER of published consumer fitness to resource quality response curves. To do so, for each dataset we plotted separately the data points below and above the TER with logged resource quality data on the X-axis, we fitted linear regressions through these data points and extracted their slopes (Supporting information). We found that in all cases the knife-edge curves were asymmetric with differences of 30–80% in the slopes on each side of the TER. The shrimp *Penaeus monodon*, the abalone *Haliotis discus hannii*, the European whitefish *Coregonus lavaretus*, and the rotifer *Brachionus calyciflorus* (data from Peñaflores 1999, Tan et al. 2001, Vielma et al. 2002, respectively, Zhou and Declerck 2019) showed a high sensitivity to nutrient limitation, while the mayfly *Ephemera sp.*, the snail *Mexithauma quadripaludium*, and three *Daphnia* species (data from Elser et al. 2006a, 2016, respectively, Frost and Elser 2002) showed a high sensitivity to nutrient excess. While the paucity of data available prevent us from comparing the specific responses of herbivores and carnivores to suboptimal resource

quality, it is clear that consumers vary in their relative sensitivities to nutrient limitation versus nutrient excess. Consumers are likely better able to cope with the nutritional imbalances they have encountered the most during their evolutionary history. Because herbivores often feed on resource having C:X ratios above their TER, we expect them to be more sensitive to low C:X (Fig. 2). Since carnivores generally consume low C:X prey or C:X prey that is similar to their own, one could expect carnivores to be more sensitive to high C:X prey. However, a recent study by Zhou and Declerck (2019) analysed the response of a planktonic rotifer to a food C:P gradient, and observed a homeostatic breakdown only at high food C:P ratios. The implication of this result for carnivores is that, if this pattern holds true for herbivores in general, carnivores may only experience variation in prey quality towards higher C:X ratios, and may have developed ways to cope with high C:X but not with low C:X prey. Hence, whether carnivores are more sensitive to stoichiometric mismatches when their prey are nutrient limited or nutrient rich is a particularly interesting conundrum which future studies should address. In this context, characterizing the stoichiometric homeostasis of resources and consumers, and linking it to the knife edge response of consumers, is a promising approach to characterize the sensitivity of herbivores and carnivores to suboptimal resource quality.

Implications

The diet composition and the optimal resource quality of herbivores and carnivores have been widely studied, but the relative sensitivity of these consumers to high and low C:X ratios has been poorly described. However, this information is crucial if we are to understand and predict how food webs will be structured and function in the future. Human activities severely alter biogeochemical cycles which, in turn, influence resource quality. Such changes may have important consequences not only for herbivores, but also for higher trophic levels of consumers. For instance, nutrient supplies directly influence the stoichiometry of autotrophs, either by changing the autotroph C:X itself, or by changing autotroph community composition and are known to affect primary consumers as well. For example, nutrient limitation at the producer level may lead to an increased somatic C:X of weakly homeostatic herbivores, and a different herbivore community composition dominated by, for example, high instead of low C:X herbivore species. Such shifts have already been observed by a number of studies (Peñuelas et al. 2012, 2013, Sardans et al. 2012, Meunier et al. 2016, Teurlincx et al. 2017), and there is the need for studies that also address responses in the performance and organismal stoichiometry of carnivores, at the individual, population and community levels.

We identified that different consumers can have different sensitivities to nutrient limitation or excess. Consequently, depending on whether resource quality shifts are towards higher or lower C:X ratios, the structure of food webs may be altered in different ways. The comparison of how taxa or functional groups from different trophic levels respond in their fitness and body elemental composition to broad resource stoichiometry

gradients is a very promising avenue that may increase our abilities to understand how community composition and food web functioning respond to changes in relative nutrient supply rates. The fact that some consumers are particularly sensitive to nutrient excess also has consequences for biodiversity patterns associated with eutrophication. In a study linking nutrient availability to consumer diversity, Evans-White et al. (2009) found that primary consumer diversity decreased steeply with increasing nutrient concentrations while the diversity of carnivores was reduced to a lower extent. This pattern could be explained by the differences in nutritional requirements and imbalances across taxa and feeding groups we discussed above, and further emphasizes the need for studies investigating the physiological processes associated with impaired fitness under nutrient excess. Because most studies so far have focused on herbivores, a promising avenue will be to characterize homeostasis regulation strategies employed by carnivores when facing imbalanced or variable resources, such as selective feeding or changes in C or nutrient excretion. Such studies on carnivores should not only offer monophagous diets with differing C:X, but also different prey types in order to broaden the range of food qualities offered to carnivores.

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Author contributions

Cédric L. Meunier: Conceptualization (lead); Methodology (lead); Writing – original draft (lead), Writing – review and editing (lead). **Maarten Boersma:** Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting). **Steven A. J. Declerck:** Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting). **Cecilia Laspoumaderes:** Conceptualization (equal); Methodology (supporting); Writing – review and editing (supporting).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

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