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The adaptive evolution of herbivory in freshwater systems

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Abstract. Herbivory is thought to be nutritionally inefficient relative to carnivory and omnivory, but herbivory evolved from carnivory in many terrestrial and aquatic lineages, suggesting that there are advantages of eating plants. Herbivory has been well-studied in both terrestrial and aquatic systems, and there is abundant information on feedbacks between herbivores and plants, coevolution of plant and herbivore defenses, mechanisms for mediating nutrient limitation, effects of nutrient limitation on herbivore life history, and, more recently, the origins of the herbivorous diet. Researchers have sufficiently defined the ecological context and evolutionary origins of the herbivorous diet, and these main areas of research have laid the groundwork for studying herbivory as an adaptation. However, we have yet to synthesize this information in a way that allows us to establish a framework of testable adaptive hypotheses. To understand the adaptive significance of this diet transition, we review the current literature and use evidence from these works as support for five hypotheses on the evolution of herbivory from carnivory: (1) intake efficiency—herbivores use part of their food source as habitat, thus minimizing the energy/time spent searching for food and avoiding predators; (2) suboptimal habitat—herbivory allows organisms to invade and establish populations in habitats that have high primary production but low abundance of animal prey; (3) heterotroph facilitation—herbivory is adaptive because herbivores consume microbes associated with producers; (4) lipid allocation—herbivory is adaptive because producers are rich in fatty acids, which fuel reproduction and storage; and (5) disease avoidance—herbivory minimizes animal-facilitated disease transmission. Due to the extensive literature, we have limited this review to discussing herbivory in freshwater systems. To our knowledge, no prior work has compiled a comprehensive list of conditions that favor an herbivorous diet in nature. With backgrounds in both theoretical and experimental ecology, the incorporation of these hypotheses to the current literature will provide information about diet evolution, where it is currently lacking.

Key words: adaptive evolution; diet evolution; freshwater herbivory; herbivory.

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INTRODUCTION

Herbivory is thought to be an inefficient feeding strategy relative to omnivory and carnivory (Sterner and Elser 2002, Laspoumaderes et al. 2010). From an energetic perspective, herbivores are important consumers because they process

primary production for use at higher trophic levels. However, at the individual level, the adaptive significance of herbivory is unclear. Omnivory is adaptive because food abundance is usually highest at lower trophic levels, whereas food quality (relative measure of energy content; defined below) increases with trophic position (Hastings

and Conrad 1979, Hairston and Hairston 1993, Elser et al. 2000, Coll and Guershon 2002, Diehl 2003, Eubanks et al. 2003). Omnivores benefit by supplementing energetically costly prey with easy to obtain, but nutritionally variable, food items (Diehl 2003). Similarly, a carnivorous diet may be adaptive because prey items are of high quality and readily digested and assimilated (Choat and Clements 1998, Stevens and Hume 2004, Raubenheimer et al. 2005). Despite the vast herbivory literature on both terrestrial and aquatic systems, comparable hypotheses of herbivory are lacking.

There are few similarities of herbivory patterns between terrestrial and aquatic systems, and as a result, these literatures have developed independently. However, the majority of herbivory work in both systems focuses on five ideas.

I. Feedback between herbivores and primary producers

Herbivores can control nutrient storage and recycling through their consumption rate of primary production (Cebrian and Lartigue 2004). In turn, herbivore consumption rates can be affected by nutrient composition of the producers (Sterner et al. 1997, Cebrian and Duarte 1998, Griffin et al. 1998, Cebrian and Lartigue 2004). These top-down and bottom-up processes drive both producer and consumer population dynamics in terrestrial and aquatic systems, although the relative strength of these forces is different between systems (see Burkepile 2013). There is a large literature (e.g., Hairston et al. 1960, Murdoch 1966, Ehrlich and Birch 1967, Slobodkin et al. 1967, Wiegert and Owen 1971, Fretwell 1977, Oksanen 1988 and others) and numerous reviews (see Power 1992, Strong 1992) on feedback mechanisms as they are one of the fundamental ideas in herbivory research.

II. Coevolution of plant and herbivore defenses

Increased plant mortality by grazers may lead to changes in the life history and population dynamics of producers. For example, many plants can produce harmful secondary metabolites in response to herbivory (e.g., Pare and Tuminson 1999, Howe and Jander 2008), but this is energetically costly (Crawley 1983) and limits energy available for other life processes (e.g., Herms and Mattson 1992). In turn, herbivores

expend energy in response to these defenses in order to obtain nutritional value from producers (e.g., detoxification pathways, Wiegand and Plugmacher 2005, Jiang et al. 2012, Zhang et al. 2012) or to defend themselves against predators (e.g., sequestering plant metabolites, Duffy and Hay 1994, Stachowicz and Hay 1999, Nishida 2002), also diverting energy from other processes. Co-evolution of these and other plant and animal defenses (e.g., altered plant morphology/phenology/nutrient composition vs. altered animal morphology/behavior/digestive physiology) has been shown to influence population dynamics of both producers and herbivores.

III. How herbivores mediate the effects of nutrient limitation

When consumers are confined to relatively poor-quality diets, they may compensate by increasing the amount of food they consume (e.g., Sinclair et al. 1982, Simpson and Simpson 1990, Targett and Targett 1990, Pennings et al. 1993, Stachowicz and Hay 1996, Cruz-Rivera and Hay 2000b, Van der Wal et al. 2000, Fink and von Elert 2006), allowing them to obtain sufficient nutrients and potentially offset the negative fitness consequences of a low-quality diet (Vanni and Lampert 1992, Cruz-Rivera and Hay 2000b, Fink and von Elert 2006). Diet selectivity has also been proposed as a mechanism to permit subsistence on the relatively poor-quality herbivorous diet (outlined in Karasov and Martinez del Rio 2007, e.g., grasshoppers, Behmer and Joern 1993, amphipods, Cruz-Rivera and Hay 2000b). Alternatively, organisms may differentially assimilate or excrete nutrients, allowing them to attain suitable quantities of limiting nutrients (Behmer 2009). Herbivores may also supplement their diets with food items of higher quality (e.g., other basal resources and/or animal prey), in order to sustain their imbalanced diet of primary food items (the “diet mixing hypothesis”; Simmonds et al. 1992, Bernays et al. 1994, Simpson and Raubenheimer 1996, Singer et al. 2002). Similarly, herbivores consuming chemically defended diets may consume other items of various qualities in order to “dilute” the toxin to benign concentrations (“toxin dilution hypothesis”; Freeland and Janzen 1974, Freeland and Saladin 1989). Herbivores may also consume less digestible items such as cellulose to increase the rate of food

passage, thereby minimizing exposure of toxins in the diet (Berg et al. 2012). These hypotheses of nutrient acquisition by herbivores and resulting life-history trade-offs (e.g., Duffy and Paul 1992, Raubenheimer and Simpson 1997, Cruz-Rivera and Hay 2000a, b, 2003, Ojala et al. 2005, Clements et al. 2009) have been a productive area of herbivory research.

IV. Effects of nutrient limitation on herbivore life history

Basal resources are variable in their nutrient content as compared to animal prey (Sternler and Elser 2002), which limits energy allocation to individual growth and reproduction of primary consumers (Mattson 1980, Lika and Kooijman 2003). A multitude of studies on herbivores from terrestrial, marine, and freshwater systems show that diet quality is linked to trade-offs among life-history traits (e.g., Rushton and Hassall 1983, Mitchell et al. 1992, Sternler 1993, Caceres et al. 1994, Hietala et al. 1995, Lampert and Trubetskova 1996, Kilham et al. 1997, Schmidt and Jonasdottir 1997, Cruz-Rivera and Hay 2000b, Shin et al. 2003, Ojala et al. 2005, Trubetskova and Haney 2006, Guo and Xie 2011, Ortiz-Rodriguez et al. 2012). Growth of an organism affects overall fitness via changes in survival and reproduction (Hairston et al. 2001), and reproductive output can have implications for population regulation (Stearns 1992).

V. Comparative analyses of related species with varying diet strategies

There are some diet characters that distinguish herbivores and carnivores. For example, postforaging food processing (i.e., digestion, assimilation) by omnivorous or carnivorous animals may be more efficient than that of herbivores (Mattson 1980, Sternler and Hessen 1994, Choat and Clements 1998, Sternler and Elser 2002), and herbivores have evolved gut morphologies that may increase food assimilation (Kramer and Bryant 1995) as a result of this processing deficit (e.g., German et al. 2010). Furthermore, “dull” teeth (e.g., German et al. 2010) or specialized feeding apparatuses (e.g., intramandibular bending; Gibb et al. 2008) may be typical of benthic herbivores. Many terrestrial studies have included digestive physiology as a characteristic of diet and recent aquatic studies have begun to do so as

well (see Choat and Clements 1998). Recent comparative studies have used these and other characters to document the evolution of herbivory from carnivorous ancestors (e.g., lizards: Van Damme 1999, Espinoza et al. 2004, mollusks: deMaintenon 1999, heteropteran insects: Eubanks et al. 2003, caddisflies: Pauls et al. 2008, fishes: Bellwood 2003, Bellwood et al. 2014), bringing us closer to understanding the adaptive significance of herbivory. These evolutionary studies are the bases for future work examining diets from an adaptive perspective.

Researchers have done a good job in delineating the ecological context and evolutionary origins of the herbivorous diet, and these main areas of research have laid the groundwork for studying herbivory as an adaptation. However, we have yet to synthesize this information in a way that allows us to establish a framework of testable adaptive hypotheses, which is a missing piece in the overall theory of diet evolution. For herbivorous lineages, at some point in time, the cumulative benefits of switching from carnivory to herbivory were greater than both the costs of doing so and the benefits of maintaining carnivory. However, carnivory remains a strategy in nature, suggesting that there are costs associated with herbivory. Similarly, the evolution of omnivory from herbivory seems beneficial, but both strategies are maintained in nature, further suggesting that there are adaptive advantages to herbivory. To understand the adaptive significance of this diet transition, we review the current literature and use evidence from these works as support for our ideas on the evolution of herbivory from carnivory (Table 1). Due to the abundant literature on this topic, we have limited this review to discussing herbivory in freshwater systems.

We propose five hypotheses that evaluate the adaptive evolution of herbivorous diets in freshwater systems (Table 1). We assume that in order for herbivory to evolve from a carnivorous ancestor, (1) there must be adequate genetic variation for herbivorous strategies to evolve and (2) the ecological relationships revealed by contemporary research are similar to those that were present in the past. Here “herbivory” is defined as the consumption of algae and/or phytoplankton and, less commonly, the consumption of aquatic vascular macrophytes (reviewed by Newman 1991).

Table 1. Description of our proposed hypotheses for the adaptive evolution of herbivory in freshwaters.

Name	Hypothesis	References
I. Intake efficiency	Aquatic herbivores may use all or part of their food source as habitat. Herbivory may allow an organism to maximize intake energy by minimizing the time spent searching for food, energy consumed during prey capture, and energy costs avoiding predators.	Brönmark and Vermaat (1998)
II. Suboptimal habitat	Herbivory may allow organisms to invade suboptimal or recently disturbed habitats. Such habitats are often characterized by having high primary production relative to consumer biomass.	For example, Proulx and Mazumder (1998)
III. Heterotroph facilitation	Herbivory may be adaptive because herbivores supplement their diets by indirectly consuming heterotrophic microbes that are associated with algae. These heterotrophs can provide nutrients that are not attainable by eating algae alone.	For example, Martin-Creuzburg et al. (2011)
IV. Lipid allocation	Some freshwater algae are sources of essential lipids and herbivorous organisms consume large quantities of these lipids relative to animal-consuming species. Because aquatic organisms use lipids for energy storage and reproduction consuming a diet rich in fatty acids may result in greater reproductive allocation. Herbivory may be adaptive because higher lipid consumption leads to higher reproductive allocation and thus, increased fitness.	Brett and Muller-Navarra (1997), Karasov and Martinez del Rio (2007), Sharathchandra and Rajashekhar (2011)
V. Disease avoidance	Animal prey may serve as intermediate hosts and facilitate transmission of parasites or prions through the diet. Herbivory may be adaptive because it reduces animal-facilitated disease transmission.	Covich et al. (1999), Marcogliese (2002)

Furthermore, “herbivore” refers to an organism that mainly eats primary producers but may indirectly consume detritus. A “carnivore” is defined as an organism that eats animals, and an “omnivore” refers to an organism that eats both plants and animals. Arguments regarding subclassifications of these diet strategies (e.g., obligate vs. facultative herbivore) or other specialized feeding strategies (e.g., wood eating, frugivory.) are not discussed here. In freshwater systems, grazers include organisms that graze algae (Feminella and Hawkins 1995, Newman and Rotjan 2013); therefore, in this study, “grazer” and “herbivore” are used interchangeably. The term “food quality” is used to describe the nutritional worth of a diet item to a consumer. Worth of a food item may be defined by macronutrient (e.g., nutritional ecology) or elemental (e.g., stoichiometry) composition, where food items are rich in protein or phosphorus, respectively. Alternatively, food quality may be defined as the ratio of food energy content to that assimilated by consumers. For both definitions, “food quality” is a relative term and can only be interpreted relative to other diets (e.g., a diet item can be both high and low quality depending on the comparison diet). The hypotheses presented here were developed to

reflect the life cycles of freshwater organisms and may or may not be applicable to organisms that do not spend their entire lives in freshwater (e.g., diadromous fishes or terrestrial insects with aquatic larvae). Although the concepts behind these hypotheses are not novel, to our knowledge, no compilation of hypotheses exists. In the following sections, we discuss the five proposed adaptive hypotheses: (1) intake efficiency, (2) suboptimal habitat, (3) heterotroph facilitation, (4) lipid allocation, and (5) disease avoidance.

ADAPTIVE HYPOTHESES

1. Intake-efficiency hypothesis

The intake-efficiency hypothesis is based on the predictions of simple optimal foraging models, which have proven robust for herbivores (Sih and Christensen 2001). This hypothesis states that selection favors herbivory over animal-containing diets because herbivorous organisms maximize energy intake by minimizing the energy and time spent searching for and subduing prey. Further, aquatic herbivores may use their food source as habitat (Brönmark and Vermaat 1998), or seek refuge in aquatic vegetation associated with their preferred food source

(e.g., submerged vegetation and epiphytic algae, respectively; Alvarez and Peckarsky 2013), thereby decreasing energy expenditures related to locomotion (Cummins 1973) and/or predator avoidance. Therefore, the net energy gained from a herbivorous diet may be greater than a diet comprised of metazoan prey.

Herbivores are constantly grazing in order to meet energetic needs (Simpson and Simpson 1990, Cruz-Rivera and Hay 2000b), whereas energetic, physiological, and encounter rate constraints prevent animal-consuming taxa from continuously foraging (Arrington et al. 2002, Karasov and Martinez del Rio 2007). As a result of these different foraging behaviors, herbivores continuously have plant material in their gut and omnivores/carnivores process their food in “batches” (discussed in Karasov and Martinez del Rio 2007). Batch processing may be followed by periods of hunger; therefore, herbivores are probably more continuously satiated relative to omnivores/carnivores. According to optimal foraging theory, satiated animals expend less energy foraging and more energy doing other activities such as mating (Krebs et al. 1983). Therefore, herbivores may gain an adaptive advantage by shifting their energetic focus from foraging to reproducing.

II. Suboptimal habitat hypothesis

The suboptimal habitat hypothesis states that herbivory may be adaptive by allowing organisms to invade suboptimal habitats. Here, the term “suboptimal habitat” is relative to habitats that support high abundance and diversity of secondary consumers. Food web interactions often occur over spatially heterogeneous landscapes (Oksanen et al. 1995), or “patches” of varying resource quality and quantity. Therefore, an optimal habitat might be a suboptimal habitat at another point in space or time. In freshwater systems, it is generally thought that habitat patches are strongly influenced by abiotic factors such as nutrient availability and/or disturbance frequency (Pringle et al. 1988). Higher trophic levels dominate communities when habitat productivity is increased (e.g., Marks et al. 2000, Deegan et al. 2002, Beveridge et al. 2010) or when disturbance occurs at low to intermediate frequencies (Marks et al. 2000). However, consuming a plant-dominated diet is favored in habitats

where animal prey are scarce and plant abundance is high (Chubaty et al. 2014), such as those with frequent disturbance. Furthermore, the palatability of plants is thought to play a key role in structuring herbivore populations (Elger et al. 2004). The most palatable benthic and phytoplankton species are associated with early stages of succession, because fast-growing plants invest less energy in structural and toxic elements (e.g., Porter 1977, Elger et al. 2004). Elger et al. (2002) investigated the effects of disturbance and nutrient availability on freshwater plant palatability for herbivorous snails (*Lymnaea stagnalis*) and found that increased disturbance frequency, but not nutrient availability, positively influenced food availability for herbivores (Elger et al. 2002), providing evidence for an herbivore advantage in disturbed habitats (e.g., suboptimal habitats).

Classic optimal foraging theory (i.e., optimal diet) predicts that if a resource is abundant, specializing on that resource is preferred (see Chubaty et al. 2014). These predictions are supported by early food preference studies, which suggest that herbivores evolved in response to food availability rather than food value (Paine and Vadas 1969). Using an evolutionary simulation model, Chubaty et al. (2014) examined how quality and availability of plant and animal prey shapes the evolution of diet. Results indicate that relative availability of resources can predict an individual's trophic level (Chubaty et al. 2014). More specifically, an increased abundance of plants increases herbivore abundance relative to carnivorous animals (Chubaty et al. 2014) demonstrating that herbivory may be adaptive when plants are abundant and prey are not (e.g., suboptimal habitats).

Seasonality can also influence habitat quality and resource availability. Organisms are limited to resources that are immediately available. Constant and seasonally varying food supplies are known to influence life histories of many aquatic consumers by altering individual growth and reproduction (output, patterns, mode, etc.). The effects of seasonal food limitation have been well studied in *Daphnia* (Tessier 1986, Chapman and Burns 1994) and other cladocerans (DeMott and Kerfoot 1982, Boersma and Vijverberg 1996). More specifically, constant food supplies are

known to increase growth and brood size of cladocerans. However, food supplies vary in nature and herbivores may gain an advantage by consuming different species or by switching between green, detrital, and/or animal diets seasonally, thereby reducing the effects of specializing on a single food type (Kitting 1980, Sanders et al. 1996, DeMott 1998, Cruz-Rivera and Hay 2000a).

Herbivory may allow organisms to minimize interspecific competition (via decreased niche overlap) by invading and establishing populations in suboptimal habitats. For example, the globally invasive golden apple snail (*Pomacea canaliculata*) specializes on freshwater macrophytes and has established successful populations in areas that are uncolonized by other phylogenetically similar species. Further, invading a suboptimal habitat may allow herbivores to escape predation. Trade-offs between foraging and predator avoidance in aquatic consumers are well documented (reviewed by Milinski 1985). Camacho and Thacker (2013) showed that freshwater amphipods exposed to fish predators sought refuge in toxic cyanobacterial mats. Further, amphipods exposed to predators showed higher survivorship on toxic mats as compared to non-toxic mats. These results suggest that herbivores at risk from predators benefit by seeking refuge in suboptimal habitats. If herbivores benefit from invading suboptimal habitats by avoiding predation, equally performing herbivores could be aggregated in both high- and low-quality patches as predicted by an "ideal free distribution" (Fretwell and Lucas 1970). Therefore, the ability to colonize and persist equally in both inferior and relatively superior habitats can promote survival of herbivores by exploiting niche opportunities that are unavailable to carnivorous species.

III. Heterotroph facilitation hypothesis

The heterotroph facilitation hypothesis states that herbivory is adaptive because herbivores indirectly consume heterotrophic microbes (bacteria, fungi, and/or protozoa) that are associated with primary producer communities. It has been shown that aquatic herbivores supplement their diets with essential nutrients originating from heterotrophic bacteria (Bowen 1984, Smoot and Findlay 2010, Belicka et al. 2012) and a strong positive correlation between primary production and

bacteria has been documented in several aquatic systems (Cole 1982). In limnetic waters, heterotrophic microbes largely contribute to planktonic biomass and are under strong grazing pressure by zooplankton (Arndt 1993). Benthic algae in close association with heterotrophic microbes come in several forms (collectively called "periphyton") and are the primary food source for herbivores in benthic systems (Wetzel 2001).

Relative to algae, heterotrophic bacteria are superior competitors for phosphorus (P), incorporating the nutrient into their cell walls (Martin-Creuzburg et al. 2011); therefore, these microbes are a rich source of the limiting nutrient for herbivores (Martin-Creuzburg et al. 2011). Although P is important for metazoan growth (Sterner and Elser 2002), diets composed only of heterotrophs are of poor quality for *Daphnia magna* suggesting that herbivores may rely on other dietary items for essential biochemicals such as sterols (e.g., invertebrates) or fatty acids (Martin-Creuzburg et al. 2011). For example, growth rates of *Daphnia magna* increased when fed heterotrophic bacteria supplemented with sterols (important for molting) relative to growth of those fed only bacteria (Martin-Creuzburg et al. 2011). Related studies found that *Daphnia* require a diet composed of at least 50% green algae to compensate for a sterol deficiency (Martin-Creuzburg et al. 2005). In a vertebrate example, the sailfin molly (*Poecilia latipinna*) was shown to assimilate both algal material and fatty acids derived from heterotrophic bacteria (Belicka et al. 2012). Consumption of heterotrophs along with consumption of autotrophs may allow herbivores to obtain adequate amounts of both P and fatty acids for growth and other life processes, respectively.

IV. Lipid allocation hypothesis

The lipid allocation hypothesis states that herbivory is adaptive because higher consumption of algae with high lipid concentrations may increase fitness. Algae are primary producers of essential lipids that cannot be synthesized by metazoans, but are necessary for their survival (Ahlgren et al. 1990, Sargent et al. 1995, Sharathchandra and Rajashekhar 2011, Guo et al. 2016). Although animal prey are rich in lipids relative to algae, wild-caught herbivorous fishes have higher lipase activities in the gut than carnivores, suggesting that lipids are of major

importance to herbivores (Nayak et al. 2003, Drewe et al. 2004, German et al. 2004).

Fatty acids can be incorporated into lipid bilayers of metazoan cells (phospholipids; Karasov and Martinez del Rio 2007), can serve as precursors for important animal hormones (Brett and Muller-Navarra 1997), and can be stored as energy (Wiegand 1996) in aquatic consumers. Excess carbon that does not originate from fatty acids can also be stored as lipid reserves in primary consumers (e.g., *Daphnia*: Sterner and Hessen 1994, Gulati and DeMott 1997), emphasizing the importance of lipid storage. In aquatic organisms, a primary role of lipids is energy storage for reproductive purposes, as they are the main components of ova (Brooks et al. 1997). During reproductive periods, lipid compounds are mobilized to the gonads in fish (Wiegand 1996, Guler et al. 2007, Wang et al. 2013) and increased dietary lipids (from 12% to 18%) result in increased fecundity (Durray et al. 1994). Lipid ingestion from algal sources has also been shown to positively correlate with reproductive success in several aquatic organisms (*Daphnia*, copepods, fishes) and with clutch size in particular (Goulden et al. 1982, Tessier et al. 1983, Schmidt and Jonasdottir 1997, Weers and Gulati 1997, Martin-Creuzburg et al. 2008, Guo and Xie 2011). In addition, organisms consuming diets rich in phospholipids allocate dietary P to ova (e.g., copepods, Laspoumaderes et al. 2010), thereby contributing to offspring growth and survival. Dietary phospholipids are the main constituents of embryonic yolk (Wiegand 1996) and thus serve as both an energy source and a component of structural growth in developing embryos (Bell 1989, Wiegand 1996). Furthermore, phospholipids are abundant in the membranes of neural tissues and are thus integral for growth of larvae, which have a high percentage of neural tissue relative to their body mass (Bell et al. 1997). As lipids (and phospholipids) are important for storage, structure, and reproduction of aquatic organisms, herbivory may be favored over omnivory and carnivory if essential lipids are obtained from available algal sources.

V. Disease avoidance hypothesis

The disease avoidance hypothesis maintains that herbivory is advantageous because it reduces disease transmission via animals. Many secondary

consumers such as piscivores are definitive hosts for parasites, with primary consumers (i.e., invertebrates or small vertebrates) serving as intermediate hosts (Covich et al. 1999, Marcogliese 2002). Furthermore, phylogenetic relatedness and similarity in biological traits between hosts has been shown to be a useful predictor of parasite prevalence in many taxa (see discussion in Huang et al. 2014). Specifically, carnivores that are phylogenetically and ecologically similar were shown to harbor similar parasite assemblages (Huang et al. 2014), suggesting that diet affects the probability of parasitic infection. Furthermore, a meta-analysis by Choudhury and Dick (2000) showed that freshwater piscivorous fishes have rich parasite communities as compared to herbivores and zooplanktivores (Choudhury and Dick 2000, see Dogiel et al. 1961, for examples). Although herbivores can contract a variety of parasites that do not originate from the diet (see Hoffman 1999 for a full review) and can experience negative effects as an intermediate host (Plaistow et al. 2001), herbivory may mediate the effects of animal-facilitated parasites and thus energy allocation to maintenance mechanisms that respond to such parasites.

Alternatively, consuming animal prey may facilitate the transmission of prions, also referred to as transmissible spongiform encephalopathies. These infectious agents are composed of protein and are responsible for mad cow disease in mammals (Dalla Valle et al. 2008). Although prions are not as common in aquatic systems as they are in terrestrial systems, prions have been discovered in some fish species (Rivera-Milla et al. 2003, Dalla Valle et al. 2008). Animal tissues are built from proteins that are potentially harmed by these agents, thereby posing a significant threat to aquatic food webs. Because basal items are not protein-rich resources (Mattson 1980, Sterner and Elser 2002), herbivores may benefit from reduced exposure to infectious prions that could alter the functioning proteins comprising their somatic tissues.

DISCUSSION

The presence of both ancestral (carnivory) and derived (herbivory and omnivory) diets in nature indicates that there are conditions that favor eating plants over animals. In support of the adaptive hypotheses presented here, the

Table 2. Assumptions of proposed hypotheses.

Hypothesis	Assumptions
I. Intake efficiency	Freshwater herbivores are relatively small and require refuge from predators, usually in the form of submerged aquatic vegetation. Submerged aquatic vegetation is associated with more palatable plants like algae that are consumed by herbivores.
II. Suboptimal habitat	Herbivores are able to detect food availability and/or quality in the current habitat and make dispersal decisions accordingly.
III. Heterotroph facilitation	Heterotrophic microbes (heterotrophic bacteria, protozoa, etc.) are in close association with freshwater primary producers and herbivores consume them indirectly.
IV. Lipid allocation	At least some essential lipids come from freshwater primary producers.
V. Disease avoidance	Parasites and prion diseases are only transmitted via animal vectors.

Note: Testing these hypotheses may be best accomplished by evaluating the assumptions necessary for them to be viable explanations for adaptive evolution of herbivory.

literature suggests that herbivory is favored when higher quality food is limiting. But, freshwater herbivore diets are not always inadequate as they can provide a different suite of important dietary elements (e.g., plant-derived lipids and sterols) that are deficient in carnivorous diets. Furthermore, these dietary elements are incorporated into both somatic and reproductive tissues and therefore may be related to fitness. Diet supplementation with heterotrophs also promotes growth and reproduction of freshwater herbivores. Testing our hypotheses will allow researchers to understand the circumstances that promote herbivory over nutritionally “better” diets.

With a few assumptions (Table 2), these hypotheses could be evaluated in current herbivory research programs. For example, the intake-efficiency hypotheses might be tested using a similar experimental design to Alvarez and Peckarsky’s (2013). They measured growth rates of two grazers (caddisfly and mayfly), algal accrual rates and per capita effects of grazers on algae in chambers that differed in the presence of moss (submerged vegetation) and predation risk. They found no differences in growth; however, when mayflies were exposed to predators, algae associated with moss accrued at a slower rate, suggesting that mayflies were using moss as both habitat and a source of food in the presence of predators. Comparable experiments could be designed to include additional life-history trait estimates (e.g., herbivore survival) and estimates of energy expenditure vs. energy gain (as in optimal foraging theory) of animals eating herbivorous vs. carnivorous diets (see Table 3, for more examples).

We present a series of hypotheses with independent explanations for each; however, these mechanisms are unlikely to function independently in nature and our knowledge of diet evolution may be limited by approaching them as such. Factorial designs evaluating multiple hypotheses and their interactions simultaneously may be more biologically relevant. For example, the heterotroph facilitation hypothesis may be tested using a design that examines the effects of diets composed of various heterotrophic: autotrophic ratios on consumer life histories (e.g., Fuller et al. 2004). Heterotrophs and autotrophs have unique lipid profiles that can be traced to consumer somatic and reproductive tissues (Iverson et al. 2004, Belicka et al. 2012). Therefore, the results from this experiment may also be explained in reference to the lipid allocation hypothesis, where consumer reproduction is affected by differential concentrations (and sources) of essential lipids in the diet. In another example, the suboptimal habitat hypothesis could be invoked in a system with high food availability and low food quality. This could be the case for *Terapontid* fishes, where availability of resources is hypothesized to be the driving force for their transition from marine to freshwater (i.e. a “suboptimal habitat”) and subsequent diet shift from carnivory to herbivory (Davis et al. 2012). This hypothesis may explain *Terapontid* invasion and shift to herbivory, but any of the remaining four hypotheses (or others not proposed here) could further explain why herbivory was maintained and continues to exist in this group. Testing these as alternative hypotheses rather than single, independent ideas may improve our interpretation.

Table 3. Examples of experimental designs that could be used as tests of our posed hypotheses.

Hypothesis	Example
I. Intake efficiency	See <i>Discussion</i> (Alvarez and Peckarsky 2013).
II. Suboptimal habitat	Jiang and Morin (2004) constructed microcosms with a productivity gradient and subjected plankton communities to invading species. Invaders and resident species increased their abundances with resource enrichment. This hypothesis could be tested by replacing herbivores as “residents” and carnivores as “invaders” and measuring herbivore and carnivore abundances as a function of increasing productivity and/or disturbance levels.
III. Heterotroph facilitation	Jäger et al. (2014) examined the interactions between <i>Daphnia</i> spp., phytoplankton and bacteria using three algal species compositions. <i>Daphnia</i> grew to high densities with a mixed diet and high light conditions. Similar field or laboratory feeding experiments could be designed by manipulating the autotrophic: heterotrophic ratio of the herbivorous diet and measuring life-history effects relative to those resulting from a carnivorous diet. A norm of reaction may be used to assess the conditions where a mixed autotrophic and heterotrophic diet is equal to or better than a carnivorous diet (in terms of fitness).
IV. Lipid allocation	Wacker and Martin-Creuzburg (2007) fed <i>Daphnia</i> spp. either algae with high lipid content or algae with low lipid content and measured lipid allocation to somatic and reproductive tissue. They found that essential lipids were preferentially allocated to offspring when provided foods with high lipid content. Gergs et al. (2014) measured growth and survival of amphipods fed diets with or without essential lipid supplementation and found that both were positively affected by the addition of lipids. Comparable feeding experiments should be conducted with these and other herbivores using natural dietary items. Life-history effects of non-herbivorous diets that vary in lipids should also be assessed. Identifying the source of lipids allocated to somatic and reproductive tissues will provide further support for the lipid allocation hypothesis.
V. Disease avoidance	Huang et al. (2014) examined factors that influence parasite sharing between carnivore hosts using a large data set on reported parasites and previously published phylogenies. They found that viruses and helminths infect phylogenetically related carnivores more than expected by chance. Similar comparative analyses could be implemented to determine patterns of parasite and prion infection across diet types.

We explained these ideas using the freshwater herbivory literature, but testing these hypotheses in other systems would complement the existing works that draw comparisons between aquatic (freshwater and marine) and terrestrial herbivory. Recent terrestrial studies have begun to elucidate the evolutionary origins of herbivory and have found similar patterns of diet evolution to those in freshwaters. For example, Reisz and Fröbisch (2014) found fossil evidence supporting the evolution of herbivorous caseid reptiles from smaller carnivore lineages and suggested that herbivory began as a way to exploit untapped resources (i.e. suboptimal habitat hypothesis). Although relative patterns of herbivory are different between terrestrial and freshwater systems (Cyr and Pace 1993, Cebrian and Lartigue 2004, Burkepille 2013), invoking comparable mechanisms for the adaptive evolution of herbivory could imply similar patterns of diet evolution across ecosystems, thereby unifying these independent bodies of work.

Herbivory has been the focus of many ecological studies spanning many subdisciplines, but there is a significant gap in knowledge

pertaining to the adaptive evolution of herbivory in nature. With backgrounds in both theoretical and experimental ecology, the incorporation of these hypotheses to the current literature will provide information about diet evolution, where it is currently lacking. The proposed hypotheses represent a starting point that may lead to more comprehensive studies of diet evolution in freshwater and other systems. Exploring these already established ideas from an adaptive perspective will establish a much-needed research framework, allowing us to more fully understand the evolution of diet in freshwater and other systems.

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